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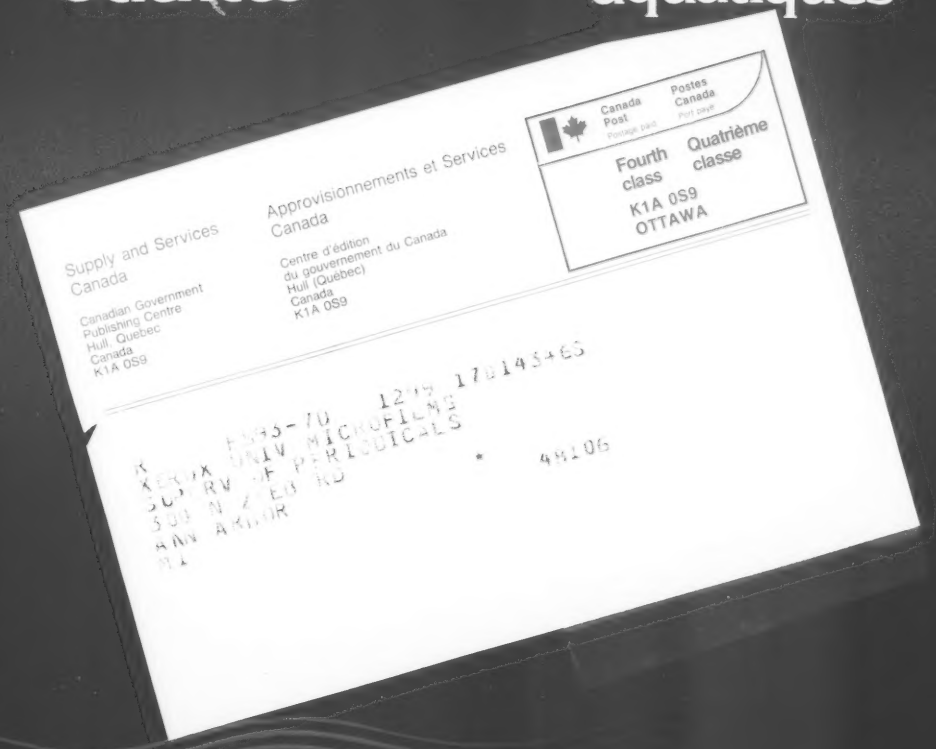

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Response and Recovery of Brain Acetylcholinesterase Activity in Atlantic Salmon (*Salmo salar*) Exposed to Fenitrothion

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Morgan, M. J., L. L. Fancey, and J. W. Kiceniuk. 1990. Response and recovery of brain acetylcholinesterase activity in Atlantic salmon (*Salmo salar*) exposed to fenitrothion. Can. J. Fish. Aquat. Sci. 47: 1652–1654.

Atlantic salmon (*Salmo salar*) parr were exposed to a number of concentrations of either technical grade fenitrothion or an operational formulation of the pesticide for 7 d or to the operational formulation for two, 24 h periods separated by 7 d. Brain acetylcholinesterase (AChE) activity decreased as concentration of fenitrothion increased. Recovery period was directly related to amount of depression, with recovery of AChE from exposure to 0.004 µL/L fenitrothion taking less than 1 wk. Samples must be taken soon after spray operations to detect exposure to such low levels of fenitrothion through AChE monitoring.

Des tacons de saumon de l'Atlantique (*Salmo salar*) ont été exposés à de nombreuses concentrations de fénitrothion de qualité technique ou à une préparation opérationnelle du pesticide pendant sept jours ou à la préparation opérationnelle pendant 2 périodes de 24 h à intervalle de 7 jours. L'activité de l'acétylcholinestérase cérébrale (AChE) diminuait à mesure que la concentration de fénitrothion augmentait. La période de rétablissement était directement liée à la baisse d'activité, le rétablissement de l'activité de l'AChE à la suite d'une exposition à 0,004 µL/L de fénitrothion s'effectuant en moins d'une semaine. Des échantillons doivent être prélevés peu après les pulvérisations afin de déceler l'exposition à ces faibles concentrations de fenitrothion par le biais de la surveillance de l'AChE.

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Exposure to organophosphorous insecticides is known to decrease the activity of brain acetylcholinesterase (AChE) in animals (Post and Leasure 1974; Fleming and Grue 1981; Roberts et al. 1988). Acetylcholinesterase activity is thought to be a sensitive indicator of organophosphate exposure. When exposure is suspected, a 20% decrease in activity relative to controls is taken as evidence that animals have been in contact with an organophosphate pesticide (Zinkl et al. 1980; Fleming and Grue 1981). Because of this sensitivity, AChE activity is used as a tool in the monitoring of exposure of organisms during forestry spray programs involving organophosphates such as fenitrothion. (Fancey et al. 1987).

ıthion (0,0-dimethyl 0-[3 methyl-4-nitrophenol] phosphorothioate) is an organophosphorous insecticide, which in Newfoundland has been used to control the hemlock looper, *Lambdina fiscellaria* (Fancey et al. 1987). It also has been widely used to control the spruce budworm, *Choristoneura fumiferana* (Symons 1977). Fenitrothion is usually sprayed aerially, with 5–7 d separating two applications of the insecticide. During spray operations, the pesticide may drift near rivers and ponds inhabited by salmonids, creating the potential for exposure of these fish to fenitrothion (Fancey et al. 1987).

Several factors seem to be involved in the amount of depression of AChE activity caused by organophosphates and the length of time required for recovery. A few studies of fish indicate that there is a greater decrease in AChE activity with exposure to higher concentrations of organophosphorous insecticides (Post and Leasure 1974, malathion; Verma et al. 1979, malathion, rogor and zolone; Klaverkamp and Hobden 1980, fenitrothion and acephate in vitro). Duration of exposure, as well as type of organophosphate and species of fish, can also affect the amount of depression of AChE activity (Weiss 1961). Recovery of AChE activity following exposure to organophosphorous insecticides has been found to take from one to more than 40 d. For malathion administered to various fish species in vivo, recovery has taken from 10–42 d (Post and Leasure 1974; Kozlovskaya and Mayer 1984; Lockhart et al. 1985). Salmonids administered fenitrothion in food required more than 27 d to recover (Wildish and Lister 1973) while those exposed to 4.61 ppm fenitrothion in water took more than 6 d to recover (Lockhart et al. 1973). Goldfish (*Carassius auratus*) exposed to DDVP in water (1.0 mg/L) recovered to normal AChE activity in 24 h (Weiss 1961). Pumpkinseed sunfish (*Lepomis gibbosus*) exposed to one concentration each of parathion, methylparathion, and azinphosmethyl took more than 4 wk to recover normal AChE activities (Benke and Murphy 1974). As well as type of organophosphate and fish species, recovery period seems to depend on the amount of depression of AChE activity with a longer recovery period required for those fish that have had a larger amount of depression in AChE (Weiss 1961; Post and Leasure 1974).

There has been little study of the effects of waterborne fenitrothion on brain AChE activities and the required recovery periods. Therefore, this study examined the dose–response relationship of brain AChE activity in Atlantic salmon (*Salmo salar*) parr exposed to sublethal concentrations of two formulations of fenitrothion. The effect of fenitrothion concentration on recovery period of brain AChE activity was also examined.

Material and Methods

Atlantic salmon parr were exposed to two formulations of fenitrothion; technical grade and an operational spray formulation. The technical formulation was 95% fenitrothion (Mobay Chemical Corp). The operational formulation was that used to control the hemlock looper in Newfoundland, Canada. It consisted of 11% fenitrothion, 40% cyclosol 63 (a solvent), and 49% insect diluent 585 (stove oil). Fish exposed to the technical formulation and their controls were 5.9 ± 0.54 cm ($\bar{x} \pm$ SD) total length, while those exposed to the operational formulation and their controls were 10.4 ± 0.89 cm.

Fish were exposed to fenitrothion in two regimens. In the first, fish were treated for seven consecutive days. They received either the technical formulation or the operational formulation. These exposures will be referred to as technical 7-d and operational 7-d, respectively. Exposures under both of these regimens were conducted in the winter. For the technical 7-d exposure, the concentrations were 0, 0.005, 0.02, and 0.16 μL/L. For the operational 7-d exposure, the concentrations used were 0, 0.04, 0.72, and 1.44 μL/L. These concentrations of the operational formulation contained 0, 0.004, 0.08, and 0.16 μL/L of fenitrothion, respectively. High Pressure Liquid Chromatography analysis of the highest and lowest concentrations used confirmed the presence of fenitrothion in the water over the entire exposure period. The 96 h LC_{50} concentration for both formulations was 1.6 μL/L of fenitrothion (Morgan and Kiceniuk 1990). Concentrations will be expressed as μL/L fenitrothion throughout, and will be given as nominal concentrations only. There are 1.33 mg of fenitrothion in 1 μL of the liquid.

In the second exposure regimen, an attempt was made to simulate a commercial application of fenitrothion. Salmon were exposed to 0, 0.04, and 1.44 μL/L of the operational formulation (0, 0.004 and 0.16 μL/L fenitrothion) for 24 h. They were then placed in clean water for 7 d before being exposed to the same concentration of fenitrothion for a further 24 h. Salmon were then given a recovery period of 0, one, or 6 wk. This will be referred to as the 2×24 h exposure regimen. This exposure regimen was conducted during the spring and summer.

Fifteen fish were treated in each concentration and recovery period, for each of the three exposure regimens. Fish were exposed to the fenitrothion in groups of five in 20 L buckets containing 10 L of aerated, fenitrothion-treated water that was changed daily. During the recovery period, salmon were held in the same buckets but with a continuous flow of water. Water temperature was ambient room temperature. For the technical 7-d exposure this was 14.7 ± 1.8°C, for the operational 7-d, 13.0 ± 1.4°C and for the 2×24 h, 15.9 ± 0.8°C. All fish were fed daily with commercial trout food.

Following exposure, fish were killed by severing the spinal column behind the opercula and were frozen, whole, at −60°C for future AChE analysis. Fish were analyzed individually except for the technical 7-d regimen, where five fish were pooled because individuals were too small to provide sufficient brain tissue for analysis. This gave a sample size of 15 except for the technical 7-d regimen which had a sample size of three; 15 fish pooled in three groups of five. Salmon brains were dissected while frozen and then homogenized, using a 2 mL glass Ten Broeck tissue grinder, in 0.05 M Tris buffer, pH 8, at a ratio of 100 mg/mL. Activity analyses of AChE were conducted at room temperature (23°C) using the method of Ellman (1961) as modified by Hill and Fleming (1982). All spectrophotometric measurements were duplicated and the average change in absorbance per minute was determined. Activity was calculated as μmoles of substrate hydrolyzed per minute per gram brain (wet weight). A pooled salmon brain homogenate, taken from fish which had not been treated in any of the regimens and which had been frozen in small aliquots for daily use, was analyzed with the experimental samples to serve as a comparison for the reliability of the assay technique. Analysis of variance (ANOVA) showed that there was no significant variation in AChE activities of this control homogenate measured on five different days ($F = 0.6$, df = 4,9 NS).

The AChE activity data were analyzed using ANOVA and Tukeys multiple comparisons (Zar 1984). The significance level was set at 0.05.

Results

AChE activity varied significantly in a typical dose–response fashion as concentration of fenitrothion increased in the 7-d exposure regimens (technical 7-d $F = 31.34$, df = 3,9 $P < 0.0001$; operational 7-d $F = 21.98$, df = 3,24 $P < 0.001$; Table 1). For the lowest concentrations used there was a difference in the percentage decline in AChE activity between the two formulations. For the technical formulation a concentration of 0.005 μL/L fenitrothion produced a 35% decline in AChE activity relative to the mean activity of the controls, while for the operational formulation 0.004 μL/L fenitrothion produced only a 12% decline in AChE activity. The highest concentrations of each formulation produced a similar decline in AChE activity, 55 and 58% for the technical and operational spray formulations respectively.

A two-way ANOVA showed that there was a significant effect of both fenitrothion concentration ($F = 61.54$, df = 2,78 $P < 0.0001$) and recovery period ($F = 32.60$, df = 2,78 $P < 0.0001$) on AChE activity, and that there was a significant interaction between concentration and recovery period ($F = 10.95$, df = 4,78 $P < 0.0001$) for the 2×24 h regimen (Table 1). Tukey's multiple comparisons showed that with no recovery period the AChE activity for those fish exposed to 0.16 μL/L was significantly less than for those exposed to 0.004 μL/L which was less than that of the controls. Following 1 wk of recovery, the AChE activity for those exposed to 0.004 μL/L fenitrothion was not significantly different from the controls and by 6 wk of recovery there were no significant differences among concentrations of fenitrothion (Table 1). Similar concentrations of fenitrothion produced a similar decline in AChE activity whether the fish were exposed for 7 d or in the 2×24 h regimen.

Discussion

Salmon parr that were exposed to fenitrothion exhibited greater decreases in brain AChE activity at higher concentrations of fenitrothion. Such a dose response has also been found for a variety of other organophosphorous insecticides (Post and Leasure 1974; Verma et al. 1979; Klaverkamp and Hobden 1980). When exposed to technical grade fenitrothion or the operational formulation containing similar concentrations of fenitrothion, similar reductions in AChE activity were observed at the highest, but not the lowest, concentrations tested. Exposure to 0.005 μL/L of the technical formulation produced a 35% decline in AChE activity while 0.004 μL/L of fenitrothion present in the operational formulation produced only a 12%

TABLE 1. Mean ± SD ($n = 15$ except 7-d technical regimen where $n = 3$) brain AChE activity of salmon exposed to fenitrothion. Letters represent results of Tukey's multiple comparisons. Within an exposure regimen, concentrations with the same letter are not significantly different. Concentrations are given in μL/L of fenitrothion. Percentages are percent of mean control AChE activity.

	7-d exposure				2 × 24 h operational exposure recovery period					
Concentration	Technical		Operational		0 weeks		1 week		6 week	
0	8.7 ± 1.1	100% A	9.4 ± 2.7	100% A	12.0 ± 1.9	100% A	12.6 ± 1.8	100% A	12.6 ± 1.6	100% A
0.004			8.3 ± 0.9	88% A	10.1 ± 1.2	84% B	13.2 ± 1.4	105% A	12.4 ± 1.0	98% A
0.005	5.6 ± 0.4	65% B								
0.02	4.8 ± 0.2	54% BC								
0.08			4.6 ± 0.5	49% B						
0.16	3.9 ± 0.6	45% C	4.0 ± 0.4	42% B	6.0 ± 0.7	50% C	8.3 ± 1.3	66% B	11.8 ± 0.8	93% A

decline in AChE. This may be the result of some difference in the formulations themselves or because of the size difference in the fish exposed to each formulation. It may be possible that the larger fish exposed to the operational formulation were less susceptible to AChE inhibition from fenitrothion exposure than the smaller fish exposed to the technical formulation.

Length of time required for recovery of AChE activity to normal was related to the amount of depression. Other studies using other organophosphates have also found that greater depression of AChE activity requires a longer recovery period (Weiss 1961; Post and Leasure 1974; Fleming and Grue 1981). This is probably because regeneration of the enzyme is mainly by de novo synthesis and when levels are depressed more, a greater amount of enzyme must be produced (Benke and Murphy 1974; Fleming 1981).

At a concentration of 0.004 μL/L of fenitrothion, recovery of AChE activity to normal required less than 1 wk, and for exposure to 0.16 μL/L, more than 1 wk but less than 6 wk was required. The maximum concentration of fenitrothion found in waterways during recent monitoring of commercial spray programs has been 0.02 μL/L, with levels usually being less than 0.005 μL/L (Mallet and Volpe 1982; Fancey et al. 1987). This study indicates that under such conditions, activities of brain AChE will quickly recover to normal levels and if exposure is to be detected, samples must be taken soon after the fish are affected. Also, our study indicates that for monitoring purposes, the sensitivity of AChE measurements is not good when exposure has been to less than 0.005 μL/L. Declines in AChE at 0.004 μL/L were only from 12–16% and were not always significantly different from the controls. Because a 20% decline in AChE activity is used as evidence of exposure to organophosphates (Zinkl et al. 1980; Fleming and Grue 1981) salmon that have encountered concentrations of 0.004 μL/L or less will not be considered to have been exposed. However, despite these shortcomings, the use of AChE activity measurements as a monitoring tool in aquatic systems should reliably detect exposure to dangerous levels of fenitrothion which might produce significant population changes.

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Influence of Sediment Disturbance and Water Flow on the Growth of the Soft-Shell Clam, *Mya arenaria* L.

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Emerson, C. W. 1990. Influence of sediment disturbance and water flow on the growth of the soft-shell clam, *Mya arenaria* L. Can. J. Fish. Aquat. Sci. 47: 1655–1663.

The importance of sediment disturbance and water flow to the production of the soft-shell clam, *Mya arenaria*, was assessed in laboratory flumes by measuring growth rates of clams exposed to a gradation of bed shear stress, free-stream velocity, and frequency and depth of sediment disturbance over a 10-m period. In the absence of sediment disturbance, growth of soft-tissue was directly proportional to both free-stream (U) and shear (U_*) velocity (r^2 = 0.64 and 0.72, respectively). It was suggested that increased organic seston flux linked higher water flow to higher growth. In all treatments, maximum growth rates were observed with daily disturbance of the top centimeter of sediment. No level of disturbance resulted in growth rates lower than those of undisturbed clams in low flow (U = 0.4 cm·s^{-1}, U_* = 0.1 cm·s^{-1}). The stimulation of growth under maximum sediment disturbance was removed when U exceeded ~3 cm·s^{-1} (U_* = 0.7 cm·s^{-1}). An energy budget for *M. arenaria* indicated that the amount of organic material suspended during sediment disturbance was insufficient to account for the increased growth in clams subjected to high levels of disturbance. It was suggested that the sediment disturbance associated with intense clam harvesting, and changes in local hydrography resulting from coastal development, may be responsible for some of the unexplained growth variation in commercial clam stocks.

Le taux de croissance de la mye comestible, *Mya arenaria*, exposée dans des canaux d'essais à une gradation de contrainte de cisaillement du lit du canal, de vitesse d'écoulement libre, de fréquence et de profondeur de perturbation du sédiment ont été mesurés pendant une période de 10 mo. Sans perturbation du sédiment, la croissance du tissu mou était directement proportionnelle à l'écoulement libre (U) et au cisaillement (U_*) à la vitesse (r^2 = 0,64 et 0,72, respectivement). D'après moi, le flux accru du seston organique liait un débit plus élevé d'eau à une croissance plus grande. Dans toutes les expériences, des taux de croissance maximale ont été observés avec la perturbation quotidienne du premier centimètre de sédiment. Aucun taux de perturbation n'entraînait un taux de croissance plus faible que celui des myes non perturbées dans une eau à débit lent (U = 0,4 cm·s^{-1}, U_* = 0.1 cm·s^{-1}). La stimulation de la croissance dans des cas de perturbation maximale du sédiment a été éliminée lorsque la valeur U était supérieure à environ 3 cm·s^{-1} (U_* = 0,7 cm·s^{-1}). D'après le bilan énergétique de *M. arenaria*, la quantité de matière organique en suspension pendant la perturbation du sédiment était insuffisante pour expliquer la croissance accrue des myes soumises à un taux élevé de perturbation. Selon moi, la perturbation du sédiment associée à une récolte intensive des myes, et des modifications du réseau hydrographique local à la suite du développement côtier, peuvent être responsables d'une partie de la variation inexpliquée de la croissance dans des stocks commerciaux de myes.

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Current speed, through its control of food supply or oxygen exchange, is a dominant physical mechanism limiting sublittoral macrofaunal productivity (Wildish 1977). For suspension-feeding epifaunal bivalves such as *Ostrea edulis* (Walne 1972), *Mytilus edulis* (Wildish and Kristmanson 1984; Fréchette and Bourget 1985a, b), *Modiolus modiolus* (Wildish and Kristmanson 1985), and *Argopecten irradians* (Cahalan et al. 1989), the linkage mechanism has been confirmed as a maintenance of food ration. Only when flows exceed a threshold velocity will decreased growth be observed due to a direct feeding inhibition (Wildish et al. 1987), inorganic dilution of suspended particulate organic matter (Gerrodette and Flechsig 1979), or clogging of filtering appendages (Rhoads and Young 1970).

For infauna, the role of flow in regulating production may be altered by an additional physical mechanism. Recent evidence has suggested that a balance between increased mortality and a nutritional subsidy resulting from sediment disturbance may regulate the productivity of the micro- and meio-benthos (Findlay et al. 1985; Palmer 1988; Emerson 1989). The combined effects of water velocity and sediment disturbance on the growth of macroinfauna are unknown. With increasing coastal development, the response of near-shore species, such as the soft-shell clam, *Mya arenaria*, to changes in flow and disturbance must be evaluated if benthic energetics are to be efficiently modelled.

The experimental control necessary to establish the response of clams to sediment disturbance and flow requires laboratory studies. Because the contact of *Mya arenaria* with the water column is limited to the sediment-water interface, two problems must be overcome if laboratory results are to be relevant to natural populations: (1) For infauna, it is not adequate to describe the flow solely in terms of U, the free-stream velocity, and (2) clams, unlike epifauna, cannot be simply positioned on the bottom of a flow chamber (e.g. Walne 1972). The velocity gradient within the boundary layer produces a stress on the bed

(τ) which can be expressed by U_*, the shear velocity: $U_* = \sqrt{\tau/\rho}$, where ρ is the density of seawater. Thus, for *M. arenaria*, U_* is an appropriate descriptor of the boundary flow. By measuring both U_* and U, the effects of water flow on clam growth can be replicated and generalized.

Ironically, to determine the effects of flow on clam growth, clams must be removed from the flow; i.e. the second problem can be eliminated by simulating the clam's natural environment within the flume. By using a skin-friction probe which measures both U and U_*, and by constructing a series of flumes, each with a natural substrate base, I have tested the null hypothesis that sediment disturbance and water flow do not account for growth variation in *M. arenaria*.

Materials and Methods

Experimental Protocol

The experimental population of 82 clams was obtained from an intertidal sandflat at Eastern Passage, Nova Scotia (described in Emerson et al. 1988). All clams were from the same cohort (4-yr-old, aver. shell length = 33.9 mm, CV = 6.8%) to remove growth variation due to age differences. Although clams from lower latitudes can reach sexual maturity at 25 mm shell length (Pfitzenmeyer 1965; Commito 1982; Brousseau 1987), clams on a nearby tidal flat reach maturity only after reaching 40 mm in length (Witherspoon 1982). In addition, the higher growth rate of these relatively small clams maximized the possibility of detecting significant changes in growth. This is particularly important in laboratory experiments in which the quality of diet is often sub-optimal, and because of the relatively slow growth rate of *Mya arenaria* in temperate latitudes (Witherspoon 1982).

To determine the effects of flow and sediment disturbance on the production of clams, net growth of individual *Mya arenaria* held in a series of flumes was measured from the end of June 1988 to April 1989. Two clams were 'planted' in each of 41 flumes containing a sediment base. The experiment consisted of seven levels of sediment disturbance (treatments). For the first, the sediment in five flumes remained undisturbed. In the remaining six treatments, increasing levels of sediment disturbance (see below) were allocated equally to the remaining 36 flumes; i.e. the first treatment was replicated five times, whereas the remaining treatments were replicated six times. A similar range of flow was allocated to each treatment; in general, each treatment had two flumes in which the flow was low (U = 0.1–2 cm·s^{-1}, U_* = 0.1–0.2 cm·s^{-1}), two flumes in which the flow was high (U = 4–6 cm·s^{-1}, U_* = 0.5–0.7 cm·s^{-1}), and two flumes in which the flow was in the mid-range (U = 2–4 cm·s^{-1}, U_* = 0.2–0.5 cm·s^{-1}). For the undisturbed treatment, however, two, one, and two flumes were allocated low, mid, and high flow rates, respectively. Ambient water temperature (1.5–16.0°C) and salinity (31 ± 1‰) were maintained throughout the experiment. The depth of the redox potential discontinuity (RPD) was 3–10 mm in each flume. Redox potential discontinuity depth was not related to flow, but was positively related to degree of disturbance (linear regression, $r^2 = 0.39$, $P < 0.01$).

Several allometric growth indices were calculated: percent increase in shell length, shell height, and shell width (length of axis joining each valve apex). These linear indices were combined to produce a fourth index, percent increase in shell-cavity volume (SC-volume), approximated by the volume of an ellipsoid. Since the direct measurement of soft-tissue growth was not possible, a final and most relevant growth index, percent increase in shell-free dry tissue weight (SFDT-weight), was measured indirectly using the relationship between shell morphometry and soft-tissue biomass. Simple linear regressions calculated between SFDT-weight and each morphometric variable indicated that SC-volume (which incorporated all linear dimensions) was the optimal predictor of SFDT-weight (log SFDT-weight (mg) = 1.03 (log SC-volume [ml]) + 1.83, $r^2 = 0.994$, $n = 202$). Although shell growth and soft-tissue growth are not always tightly coupled (Hilbish 1986; Borrero and Hilbish 1988), shell growth has been used as a practical measure of bivalve production (Nielsen 1985; Peterson and Fegley 1986). In addition, bias common with direct weight measurement of *Mya arenaria* (Hawkins and Rowell 1987) is eliminated by indirect estimation.

Flume Design

The dimensions of each flow-through flume were restricted to minimize the demand on water supply (Fig. 1). The objective in flume design was to provide a range of flows (~0.1–6 cm·s^{-1}) in a smooth–turbulent boundary layer. Critical shear velocities of Eastern Passage sediment were not exceeded in the flumes ($U_{*crit} < 0.95$ cm·s^{-1}: Grant et al. 1986), and minimum flows were observed to be sufficient to maintain both an aerobic sediment–water interface, and water and sediment temperatures equivalent to those in flumes of higher flow. Free-stream velocity was defined as the 10-s average of water velocity 1.5 cm above the sediment. Shear velocity was measured at the sediment–water interface adjacent to each siphon. Both U_* and U were measured using a skin friction probe with an accuracy of ±10% and a minimum threshold of U_* = 0.1 cm·s^{-1} (Gust 1987).

Filtered seawater, provided by the Dalhousie Aquatron facility, was pumped into each flume through a T-shaped, perforated diffuser facing the bottom of the intake reservoir. Turbulence was homogenized further by directing flow through a screen (baffle thickness = 1 cm, mesh size ~3 mm). Exit conditions consisted of a perforated plate, a compromise between a solid weir which can produce upstream non-conformities in the boundary layer, and a free fall, which requires a larger water supply and restricts water depth in low flows. Water depth in all flumes was 2.5 cm (± 3 mm). Uniformity of flow in the test section was created by the 4:1 ratio of flume width to water depth. With this ratio, and a side-wall boundary roughness lower than that of the sediment, secondary circulation and side-wall boundary-layer effects were reduced (see Nowell and Jumars 1987).

The bottom of each flume was covered by a 12 cm deep layer of sieved (1 mm mesh) sediment from the Eastern Passage intertidal flat. Mean grain size after sieving (220 μm) was similar to that of Eastern Passage sediment (200–250 μm). Sediment depth in each flume was greater than that required by clams to attain their natural living depth within the sediment (Emerson et al. 1988). Clam densities in the flumes were 50% lower than those at Eastern Passage (Emerson et al. 1988). During planting, clams were oriented so that the inhalent–exhalent siphon axis was perpendicular to the direction of current to prevent pumping of exhaled water (Vincent et al. 1988). Clams were progressively offset from the flume's midline to limit downstream effects by the upstream clam. The distance between the inlet and the upstream clam, and that between the two clams

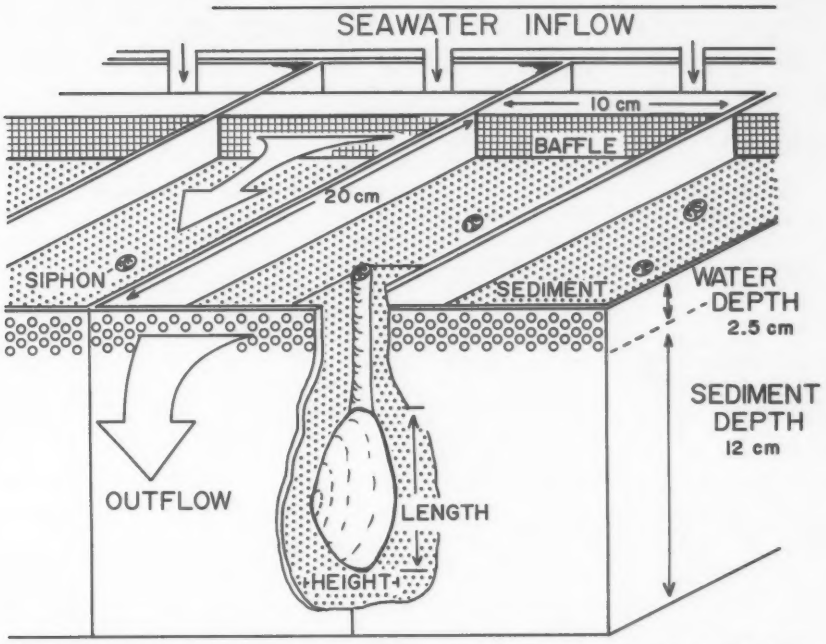

FIG. 1. Schematic representation of experimental flumes. Position of clam (size not to scale) is shown in the cut-away section. Total number of flumes was 41.

in a flume, were both ~6 cm. All clams were acclimated to the seawater system for 1 wk prior to planting, and to the flumes for an additional week prior to sediment disturbance.

Every 3 d, clams were fed a diet of ground (to 300 μm), dry cereal in suspension (15 $J \cdot g^{-1}$ cereal: 17% protein, 2% lipid, 81% carbohydrate); ration was approxiately 30% of clam SFDT-weight. Diet was supplemented by phytoplankton (*Chaetoceros gracilis*; ~2% of tissue weight) once per month. Food addition lasted approximately 10 min, during which flume inflow was reduced to 10% of normal flow rate.

Application of Sediment Disturbance

To isolate the effect of sediment disturbance from that of water flow, it was necessary to maintain subcritical shear velocities in the flumes. Sediment was artificially disturbed by injecting water into the sediment surface through a T-shaped sprinkler head of equivalent width to each fiume. The entire sediment surface was raked by manually directing the water jets into the sediment surface for 10 s, during which flume outflow was reduced to 50% of normal flow rates. By adjusting sprinkler pressure, the top one or 10 mm of sediment could be disturbed. Depth of disturbance was determined by directing the sprinkler into a sediment core consisting of alternating 2 mm deep layers of white and dark sand, and visually detecting the maximum depth of disturbance.

Depths and frequencies of sediment disturbance were chosen to reflect natural time and spatial (vertical) scales of sediment transport at Eastern Passage (C. W. Emerson, unpubl. data). Combinations of frequency (absent, monthly, weekly, daily) and depth of sediment disturbance (0 mm, 1 mm, 10 mm) comprised a sediment disturbance hierarchy (Table 1) which was used in all statistical analyses. In the mid-range (Degrees 3–5), it was assumed that frequency rather than depth was the dominant component of disturbance. Thus, the level of sediment disturbance from monthly, deep raking was less than that of shallow, weekly raking.

TABLE 1. Frequency, approximate depth, and degree of sediment disturbance in flumes containing *Mya arenaria*. The hierarchy of sediment disturbance (Levels 1–7) was used in all statistical analyses.

Frequency of disturbance	Depth of disturbance	Degree of disturbance	Level
Absent	0 mm	Lowest	1
Monthly	1 mm		2
Monthly	10 mm		3
Weekly	1 mm	↓	4
Weekly	10 mm		5
Daily	1 mm		6
Daily	10 mm	Highest	7

Results

For the entire experimental population, the mean initial shell length (33.9 mm, CV = 6.8%), height (20.7 mm, CV = 7.1%), and width (12.5 mm, CV = 7.1%) increased by 3.7% (CV = 96.8%), 5.6% (CV = 67.0%), and 3.2% (CV = 19.1%), respectively, after 10 mo. Mean percentage increase from both initial shell cavity volume (4.6 mL, CV = 19.1%) and SFDT-weight (330.9 mg, CV = 19.6%) was 13% (CV = 88%). Mortality (<7% over 10 mo) was not related to flow rate or level of sediment disturbance. Analyses of results were partitioned into the determination of (1) the effects of flow (U and U_*) on growth in the absence of sediment disturbance, and (2) the interactive effects of sediment disturbance and flow on growth.

Whereas the first objective could be met by relatively simple linear regression analyses, the second objective required analysis of covariance (ANCOVA) and a multiple comparison technique. For the ANCOVA, clam growth was the dependent variable, level of sediment disturbance (1–7) was the factor, and water flow (either U or U_*) was the covariate. To isolate any significant effects identified by ANCOVA, the GT2 multiple comparison method was used.

Sokal and Rohlf (1981) have recommended the GT2 method to test for significant differences among means adjusted for the covariate. In this technique, a minimum significant difference (MSD) was calculated for each adjusted mean: MSD = (critical value) × (standard error of the adjusted mean), where critical value refers to the statistical distribution appropriate to a given test, in this case, the studentized maximum modulus. If comparison intervals ($\text{mean}_{adj} \pm \text{MSD}$) did not overlap, means were considered to be significantly different. For a detailed explanation of this technique, refer to Sokal and Rohlf (1981: p. 242–252). Effects of flow and sediment disturbance on growth were illustrated further using a kriging procedure (see below). To normalize the distributions and homogenize the variance, all growth indices were arcsine-transformed, and the flow variables were log-transformed.

Water Flow and Clam Growth

The experimental design allowed the measurement of flow effects on clam growth in the absence of sediment disturbance. Simple linear regressions were calculated between the percentage growth in SFDT-weight and both flow variables (Fig. 2). In separate regressions, free-stream velocity and shear velocity explained 64% and 72%, respectively, of the variation in clam growth. Over the range of flows tested (U = 0.1–5.8 cm·s^{-1}, U_* = 0.1–0.5 cm·s^{-1}), there was no evidence of growth inhibition; growth was directly proportional to flow. Because shear velocity was highly correlated with, indeed dependent upon, free-stream velocity (r^2 = 0.80), it was impossible to determine the independent effects of U and U_* on clam growth. Nonetheless, it appeared that shear velocity was a better predictor of clam growth than free-stream velocity.

An effect of clam position (upstream or downstream) on clam growth could not be discerned by ANCOVA, using position as the factor and U or U_* as the covariate ($P > 0.05$). As a result, the preceding regressions were calculated irrespective of clam position. Regressions using the other growth indices all showed the same trend with U and U_* as the SFDT-weight growth index. For conciseness, these additional flow–growth relationships were not illustrated. Coefficients of determination for these additional regressions with free-stream velocity were 0.42, 0.38, 0.64, and 0.62 for shell length, height, width, and cavity volume growth indices, respectively.

Effects of Sediment Disturbance on Clam Growth

With free-stream velocity as the covariate, significant differences in growth resulting from sediment disturbance were found for all growth indices, with the exception of shell height (Table 2). Because of the non-significant relationship between the growth in shell height and sediment disturbance, it could not be assumed that the growth of SC-volume would be sig-

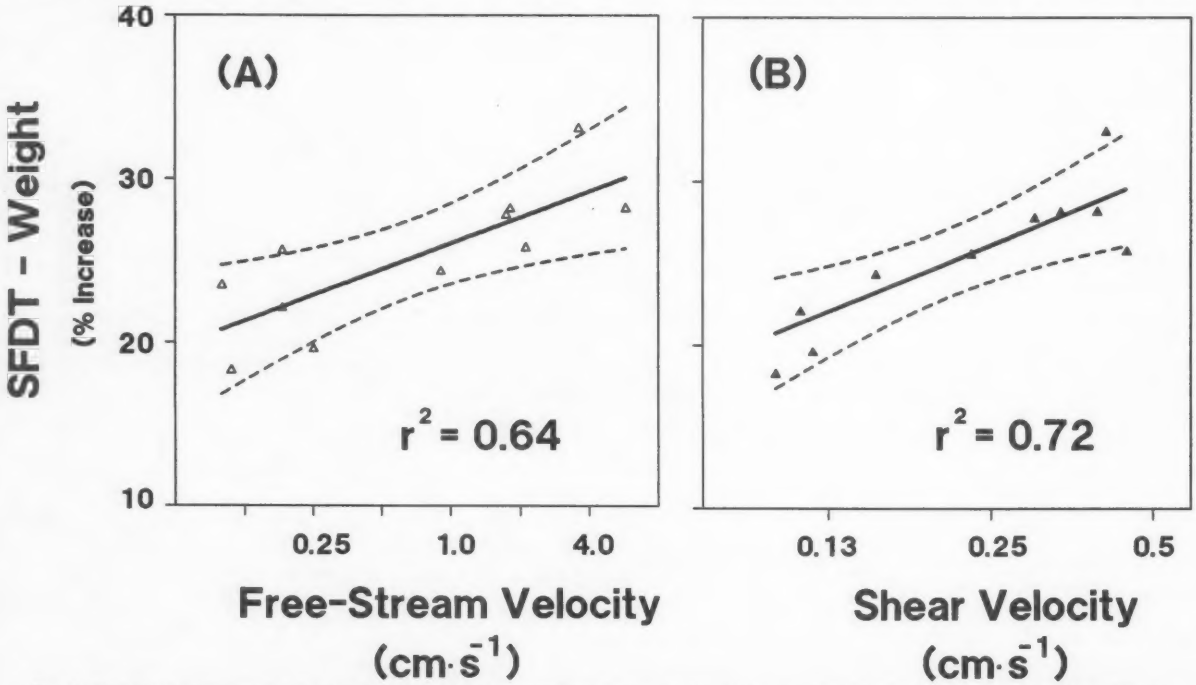

FIG. 2. Simple linear regressions calculated between (A) the percentage increase in shell-free dry tissue weight of *Mya arenaria* and free-stream velocity, and (B) weight increase and shear velocity. Data included only those clams which grew in the absence of sediment disturbance (over a 10-mo period). Coefficients of determination and 95% C.L. are indicated. Sample size was 10 for both regressions. SFDT-weight has been arcsine-transformed and flow variables were plotted on a logarithmic scale.

TABLE 2. *F* statistics from ANCOVA tables indicating the response of clam growth to sediment disturbance, with either free-stream or shear velocity as the covariate. As a prerequisite to ANCOVA, results of tests for homogeneity of slopes are indicated. * $0.05 \geq P > 0.01$; ** $0.01 \geq P > 0.001$; *** $0.001 \geq P$; NS = Not significant.

		Treatment	Covariate	
Growth index	Homogeneity of slopes	Sediment disturbance	Free-stream velocity	Shear velocity
Shell length	1.39 NS	3.03 *	10.89 **	
	0.48 NS	2.58 *		4.82 *
Shell height	1.24 NS	1.26 NS	8.30 **	
	0.22 NS	1.12 NS		2.32 NS
Shell width	1.88 NS	7.58 ***	32.79 ***	
	1.09 NS	5.38 ***		13.08***
SC-volume	1.72 NS	4.15 ***	18.16 ***	
	0.45 NS	3.19 **		6.73 *
Soft-tissue	1.70 NS	4.15 ***	18.09 ***	
Weight	0.45 NS	3.19 **		6.72 *
Condition	1.21 NS	1.45 NS	1.15 NS	
index	1.01 NS	1.48 NS		1.04 NS

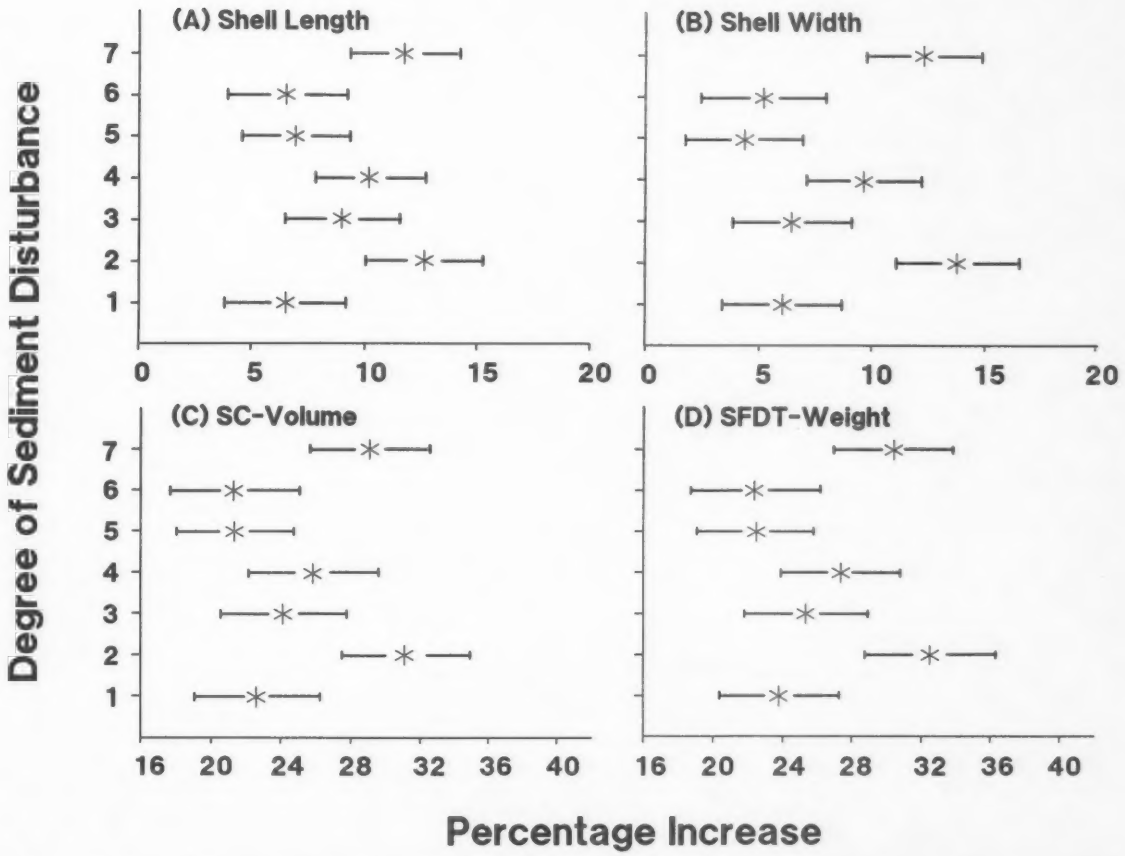

FIG. 3. Mean clam growth adjusted for shear velocity (covariate) at all levels of sediment disturbance. The levels of sediment disturbance are defined in Table 1. The horizontal bars represent 95% comparison intervals (GT2 method). Means whose intervals overlap were not significantly different. The shell-height growth index was not included because ANCOVA results indicated a non-significant relationship with sediment disturbance. SC = shell cavity, SFDT = shell-free dry tissue.

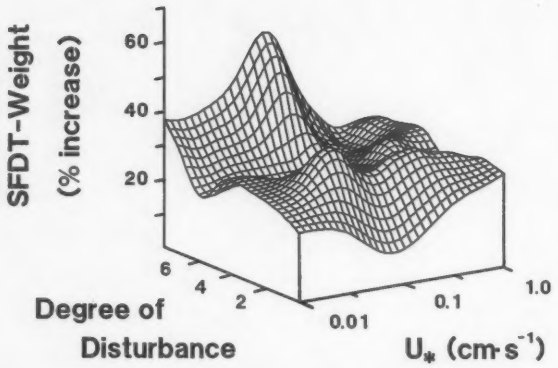

FIG. 4. The relationship between percentage growth in shell-free dry tissue weight, degree of sediment disturbance, and shear velocity (U_*), predicted from a distance-weighted, least-squares kriging model. The levels of sediment disturbance are defined in Table 1.

nificantly linked to degree of disturbance. It appeared, however, that the increase in length and width compensated for shell height, since a significant relationship was calculated between SC-volume and sediment disturbance. With shear velocity as the covariate, all growth indices were significantly related to the degree of sediment disturbance, with the exception of the percentage increase in shell height. In most cases, however, the levels of significance calculated using the shear-velocity covariate were lower than those using free-stream velocity.

The GT2 multiple comparisons revealed that the effect of increasing sediment disturbance on clam growth was not uniform (Fig. 3). (Since multiple comparison results for U and U_* covariates were identical, only treatment effects adjusted for U_* are shown.) A bimodal distribution of comparison intervals was observed for all growth indices. Although there was a large amount of overlap, four distinct components appeared within each distribution. First, undisturbed clams grew approximately 8% less than those which experienced the minimum degree of sediment disturbance. Second, an increase in disturbance from Degree 2 to 3 generally resulted in a slower growth rate, although a statistically significant decrease was found only for the shell width growth index (Fig. 3B). Third, although there appeared to be a further general trend of decreasing growth with increasing degrees of sediment disturbance (Degree 3–6), there were no significant differences between the growth of clams subjected to monthly disturbances of 10 mm depth (Degree 3) and that of clams disturbed daily at 1 mm depth (Degree 6). Lastly, clams exposed to the maximum degree of sediment disturbance (Degree 7) grew approximately 8% larger than clams under daily, shallow disturbance (Degree 6). The effect of maximum sediment disturbance was not significantly different from that of minimal disturbance (Degree 2).

The combined effects of water flow and sediment disturbance on soft-tissue growth of *Mya arenaria* were illustrated using a distance-weighted, least-squares kriging program (Wilkinson 1988: Fig. 4). By providing an objective method of data interpolation, such programs are useful for identifying general trends (Gilbert and Simpson 1985), especially when the results of ANCOVA and GT2 analyses can be used as interpretive guides. Kriging was particularly useful in the present study since the interactive effects of flow and sediment disturbance on clam growth were difficult to visualize using only ANCOVA and GT2 analyses. Interpretation of surface topography in the model generated for the SFDT-weight growth index was restricted to the area covering the higher flows ($U_* \geq 0.1$ cm·s^{-1}) because of the low accuracy of the skin-friction probe in minimal flows (Gust 1987).

Maximum growth rates (60% increase) were observed for clams subjected to maximum sediment disturbance under low flows ($U_* = 0.1$ cm·s^{-1}). As degree of disturbance decreased at this level of flow, the bimodal pattern first indicated by the GT2 analysis was observed. Minimal growth rates (10% increase) were indicated for undisturbed clams in low flow. The growth rate of clams subjected to disturbance was frequently greater, and never less, than that of undisturbed clams. As indicated by the simple linear regressions (Fig. 2), clam growth was directly proportional to shear velocity ($U_* = 0.1$–0.7 cm·s^{-1}) in the absence of disturbance. Over the same range of U_*, but at maximum levels of disturbance, clam growth was inversely proportional to shear velocity. Allocation of significance to the remaining surface features was not warranted.

Non-Treatment Effects on Clam Growth

Difficulties of simulating natural conditions in the laboratory can lead to abnormally high levels of non-treatment stress which may restrict the extrapolation of laboratory results to natural populations. In addition to the low mortality in the experimental population, minimal laboratory stress was reflected by the comparable growth rates of experimental clams and those in a nearby field population. Published parameters for the Von Bertalanffy growth equation (Eq. 1) were used to predict the increase in shell length of the experimental clams if they had remained in the field:

$$(1) \quad L_t = L_\infty (1 - e^{-k(t - t_o)})$$

where L_t = a given shell length, L_∞ = length at which growth rate is zero, k = growth rate to L_∞, t = age (yr) at given length (from *annual* shell growth rings), and t_o = age at which length is zero. On a nearby clam flat, Chezzetcook Harbour N.S., $L_\infty = 127.880$ (SE = 3.73), $k = 0.063$ (SE = 0.0025) and $t_o = -0.688$ (SE = 0.0259) (Witherspoon 1982). The predicted in situ shell growth is 12.0% over 10 mo, however, this rate does not reflect the seasonal growth variation observed in bivalves (Hilbish 1986; Peterson and Fegley 1986). For *Mya arenaria*, growth during the seasons over which the experiment was conducted (late summer, fall, and winter) is only 30% of annual growth (Newcombe 1935). As a result, a more reasonable estimate of growth under natural conditions would be 3.6%, an increase which corresponds to that observed in the experimental population (average = 3.7%).

Condition index analysis also indicated minimal laboratory stress. The allometric condition index (ACI) is useful as a rapid assessment of the ecophysiological status of bivalves: ACI = SFDT-weight/SC-volume (Brown and Hartwick 1988; Bonsdorff and Wenne 1989). A decrease in the ACI often reflects deficits resulting from environmental stress. On average there was only a 10% decrease in the ACI of the experimental population after 10 mo (from an initial mean ACI of 71.4, CV = 6%). ANCOVA results indicated that this reduction was common to all experimental clams (Table 1); each treatment was affected equally by non-treatment stress.

Discussion

Effects of Flow on Growth Rate

If food-limited, suspension feeders will benefit from the increased organic seston fux of higher flows until a critical

velocity (U_{crit}) is reached, beyond which growth is inhibited. Wildish et al. (1987) have demonstrated that for *Placopecten magellanicus*, $U_{crit} = 10$ cm·s^{-1}, and Eckman et al. (1989) have shown that the growth of *Argopecten irradians concentricus* at $U = 17.2$ cm·s^{-1} was significantly less than at $U = 1.4$–8.6 cm·s^{-1}. Under the low flows of the present study ($U_{max} < 6$ cm·s^{-1}), it would appear that the positive correlation between growth of *Mya arenaria* and water velocity (in the absence of sediment disturbance) was a simple consequence of a nutritional subsidy. However, the experiment was designed to specifically exclude this mechanism linking growth to water flow.

By ensuring that the clams were not food-limited, it was intended that factors other than food supplementation might be identified as being responsible for higher growth in higher flows. Unfortunately, the difficulty in maintaining an optimum food ration in flow-through systems over prolonged periods may have produced food-limited conditions. This situation was confounded by the discovery of a continuous addition of organic seston (e.g. algal cells, bacteria, detritus) via the 'filtered' seawater system. Although these particles were small (≤ 30 μm), bivalves have been shown to efficiently utilize particles smaller than 10 μm (Riisgård 1988).

The concentration of total seston in the flume water column was found to be 1.5 mg dry wt·L^{-1} (CV = 82%), which translates into a minimum flux (flumes with lowest flows) of at least 13 mg·hr^{-1}. Even if one assumes an abnormally low organic content for this seston (~40% by weight), it appears likely that natural seston in the seawater system provided the bulk of the food ration. Therefore, clams in higher flows experienced a greater seston flux and, consequently, a greater growth potential than clams in low flows. This is consistent with a recent field study in which horizontal seston flux was concluded to be a major factor affecting growth of another infaunal suspension-feeding bivalve, *Mercenaria mercenaria* (Grizzle and Morin 1989).

It should be noted that a seston depletion effect (Wildish and Kristmanson 1985), when downstream clams receive signficantly less seston than upstream ones, was unlikely. An effect of clam position on the growth of clams (in the absence of sediment disturbance) could not be detected by analysis of covariance. Calculations of water flow and clam pumping rate support this conclusion. In flumes having the lowest free-stream velocities (~0.1 cm·s^{-1}), the flux of water through the flume was approximately 9 L·hr^{-1}. The maximum pumping rate determined for *Mya arenaria* is 3.9 L·hr^{-1}·g^{-1} SFDT-weight (Jørgensen and Riisgård 1988). Using the SFDT-weight of the largest clam in the present study (487.7 mg), the maximum combined pumping rate of two clams in one flume was only 3.8 L·hr^{-1}, well below the slowest flow rate. I suggest, therefore, that upstream clams had little or no effect on the growth of downstream clams with respect to seston depletion.

Further insight into the mechanisms governing flow and growth could not be deduced from measures of shear velocity in this experiment; the independent effects of U_* and U on clam growth could not be differentiated because of the high dependence of U_* on U. The primary value of U_* measurement was in the simulation of natural flow conditions and to provide a standard of comparison with future studies. As the independent variable, U_* is preferable to U since the clams experience shear stress rather than the bulk layer flow. It was not surprising, therefore, that U_* was a better predictor of clam growth than U, in the absence of sediment disturbance.

Effects of Sediment Disturbance on Growth Rate

Empirical models have suggested that the general negative correlation between hydrodynamic forcing and the production of many benthic communities is partly a response to sediment movement (Emerson 1989). This is in direct contrast to the observation in the present study that *Mya arenaria* grew fastest under the highest degree of sediment disturbance, and did not exhibit a significant decrease in growth rate under any degree of disturbance. Because the models incorporated flows beyond U_{*crit} for long periods, this discrepancy may be a simple result of scale differences between the models and the present study. Moreover, Emerson's size-specific models indicated that the general negative relationship between growth and sediment disturbance was much less significant for macrofauna than for smaller organisms, presumably because macrofauna are more resistant than micro- and meio-fauna to mortality caused by abrasion and erosion due to sediment movement (cf. Munro et al. 1978; Palmer 1988; Miller 1989). Nonetheless, high clam growth at a relatively high level of sediment disturbance was unexpected.

Mya arenaria is very sensitive to mechanical and other stimulation (Jørgensen and Riisgård 1988). When disturbed, the valve gape is reduced and the siphon and mantle edges are retracted, thereby reducing pumping and ingestion rates. Apparently, this stress was subordinate to the benefits of sediment disturbance. The few examples describing a positive relationship between sediment disturbance and the benthos have usually involved entire communities (via recruitment: Fegley 1988), or with the microfauna (via nutrient supplements: Findlay et al. 1985), but not, until now, with individual macrofauna.

The most likely mechanism for growth enhancement of *Mya arenaria* under sediment disturbance was a food subsidy from resuspended particulate organic matter (POM). High concentration of benthic algae, microfauna, and detritus in the top centimeter of sediment were made available as a result of sediment disturbance (see Wildish 1977). This is consistent with the evidence of flow-disturbance interaction (Fig. 4); additions of POM during disturbance were of greatest benefit under slow flow. This benefit was removed with a decrease in the residence time of POM (i.e. under higher flows) probably because clams could not utilize the POM before this food was flushed from the flume.

Although a nutritional link between disturbance and growth appeared reasonable, the construction of a simple energy budget rejected the above hypothesis. Sediment disturbance added a maximum of 15 mg dry wt of organic matter to the water column, but during the 7 min required for clams to resume normal pumping activity, the food supplement was reduced to a maximum of 1 mg POM. Even if the clams were able to utilize ~50% of the supplement (an overestimate given the relatively high flume flow rates and low clam pumping rates), clams subjected to the maximum degree of sediment disturbance would receive a maximum food supplement of only ~150 mg dry wt organic matter over 10 mo. If I assume a maximum gross growth production efficiency of 6% (for infaunal suspension feeders; Bayne and Newell 1983), this supplement could not account for the entire growth increase (~26 mg soft tissue) in clams subjected to daily, deep sediment disturbance relative to clams under daily shallow disturbance. Further, it is obvious that a food supplement from disturbance could not have

accounted for the higher growth in clams subjected to monthly, shallow disturbance relative to that of undisturbed clams.

It is possible that sediment disturbance indirectly provided an energetic subsidy by influencing the growth of other, smaller organisms within the sediment (Findlay et al. 1985), however, it is not clear how this production would become available to the clams. In summary, high-frequency, low magnitude sediment disturbance may provide a positive, (rarely a negative), growth potential for natural populations of *Mya arenaria*. Experimental limitations and the complexity of the problem have precluded identification of the link between disturbance and growth, however, it is possible that a mechanism other than a food subsidy may exist.

Implications to Natural Clam Populations

Results from these flume experiments have identified two factors by which coastal development and fishing pressure may indirectly influence the growth of clam populations. With the construction of a proposed tidal-power barrage in the upper Bay of Fundy, Wildish et al. (1986) have predicted a 50% decrease in shear stress exerted on a major clam tidal flat (see Witherspoon 1984). In addition to changing sedimentation patterns, results suggest that a lower shear stress may reduce the amount of suspended food available to the clams and favour a shift to a deposit-feeding community (Wildish and Peer 1983). These changes may not be entirely negative; while hydrographic changes may reduce the food supply to one clam flat, another may be favoured.

Increases in fishing effort may also be indirectly responsible for variation in clam population growth, but again, an entirely negative effect on the population is not necessarily implied. Removal of market-size (sexually mature) clams may be offset by the potential for increased growth under the increased level of sediment disturbance typical of commercial clam flats. This phenomenon may partially account for the unexpected observation that clams survive to the pre-recruit and recruit stages much better in areas which are heavily fished than in areas closed to fishing (Angus et al. 1985). It is likely that modelling of clam population growth will improve with the inclusion of sediment disturbance and water flow as potential predictor variables.

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Testing a Bioenergetics-Based Habitat Choice Model: Bluegill (*Lepomis macrochirus*) Responses to Food Availability and Temperature[1]

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Using an automated shuttlebox system, we conducted patch choice experiments with 32, 8–12 g bluegill sunfish (*Lepomis macrochirus*) to test a behavioral energetics hypothesis of habitat choice. When patch temperature and food levels were held constant within patches but different between patches, we expected bluegill to choose patches that maximized growth based on the bioenergetic integration of food and temperature as predicted by a bioenergetics model. Alternative hypotheses were that bluegill may choose patches based only on food (optimal foraging) or temperature (behavioral thermoregulation). The behavioral energetics hypothesis was not a good predictor of short-term (from minutes to weeks) patch choice by bluegill; the behavioral thermoregulation hypothesis was the best predictor. In the short-term, food and temperature appeared to affect patch choice hierarchically; temperature was more important, although food can alter temperature preference during feeding periods. Over a 19-d experiment, mean temperatures occupied by fish offered low rations did decline as predicted by the behavioral energetics hypothesis, but the decline was less than 1.0°C as opposed to a possible 5°C decline. A short-term, bioenergetic response to food and temperature may be precluded by physiological costs of acclimation not considered explicitly in the behavioral energetics hypothesis.

A l'aide d'un système de boîte automatique, nous avons effectué des expériences de choix de parcelles avec 32 crapets arlequins (*Lepomis macrochirus*), pesant de 8 à 12 g, afin de vérifier une hypothèse d'énergie de comportement relativement au choix de l'habitat. Lorsque la température et la quantité d'aliments de la parcelle à l'étude sont maintenues constantes dans les parcelles mais qu'elles sont différentes d'une parcelle à l'autre, nous nous attendions à ce que les crapets choisissent les parcelles qui favorisent au maximum la croissance en nous fondant sur le principe de l'intégration bioénergétique des aliments et de la température telle que prévue par un modèle bioénergétique. Selon d'autres hypothèses, les crapets peuvent choisir des parcelles seulement en fonction de la nourriture (broutage optimal) ou de la température (thermorégulation comportementale). L'hypothèse de l'énergie du comportement n'était pas un bon élément de prédiction du choix à court terme des parcelles (de minutes à semaines) par les crapets; l'hypothèse de la thermorégulation du comportement était le meilleur élément de prédiction. A court terme, il semblait que la nourriture et la température modifiaient le choix de la parcelle hiérarchiquement; la température était la plus importante bien que les aliments puissent modifier les préférences au niveau de la température pendant les périodes d'alimentation. Au cours d'une expérience de 19 jours, les parcelles à température moyenne fréquentées par les poissons offrant de faibles rations alimentaires ont effectivement diminué conformément aux prédictions de l'hypothèse d'énergie du comportement, mais la diminution était inférieure à 1.0°C par opposition à une baisse possible de 5°C. A court terme, la réaction bioénergétique à l'alimentation et à la température peut-être exclue par les coûts physiologiques de l'acclimatation qui ne sont pas considérées explicitement dans l'hypothèse de l'énergie du comportement.

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Food, as it influences habitat choice, has been explored with optimal foraging theory (Pyke 1984). In this theory, fish are assumed to choose habitats based on the net rate of energy intake, which is thought to be related to fitness (Pyke 1984). Many studies of foraging behavior have shown that fish deal efficiently with the differential availability of food in their environment (Murdoch et al. 1975; Mittelbach 1981; Dill 1983; Werner et al. 1983; Mittelbach 1984; Crowder 1985). The effects of temperature on habitat choice are relatively well known (e.g. Neill and Magnuson 1974; Coutant and Carroll 1980). In laboratory studies fish spend about two-thirds of their time within 2°C of their final preferred temperature (Magnuson et al. 1979; Mathur et al. 1981); fish thereby occupy temperatures favorable for the joint conduct of life processes and thus enhance fitness (Brett 1971; Beitinger and Fitzpatrick 1979; Neill 1979). Both food and temperature, thus, play major roles in the bioenergetics and growth of fish (Brett 1971; Magnuson et al. 1979), but little is known about the interaction of their effects on habitat preferences (Crowder and Magnuson 1983).

Under natural conditions, fish often must respond to both food and temperature as well as other factors in making habitat choices (Neill and Magnuson 1974; Ware 1982; Crowder and Magnuson 1983). One way to address this problem is to incorporate the costs and benefits of all these factors into one model; for the combination of food and temperature, this integration

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may be achieved using fish bioenergetics models (Kitchell et al. 1974; Kitchell et al. 1977; Stewart et al. 1981, 1983). The effectiveness of these models in predicting fish growth based on food and temperature has been independently tested (Rice and Cochran 1984) and sensitivity analyses have determined how model predictions respond to parameter uncertainty (Bartell et al. 1986). Fish bioenergetics models are generally well-documented and can reliably predict the long-term effects of food and temperature on fish growth.

Physiologists and ecologists are interested in how ectotherms, including fishes, might respond behaviorally to food and temperature and whether or not observed distributions of fish are predictable (Brett 1971). Brett described the vertical migration of sockeye salmon (*Oncorhyncus nerka*) in lakes and suggested that this behavior conferred bioenergetic benefits. Growth of sockeye in fixed and fluctuating temperature regimes also suggests a bioenergetic benefit to vertical migration when fish are held at intermediate rations (Biette and Geen 1980). Vertical migration in young sockeye has also recently been interpreted as due to predator avoidance (Clark and Levy 1988), so even this well-cited case has not been clearly resolved.

That bioenergetics drives behavioral decision-making in fishes is an intriguing idea which has been reasonably well examined (Ware 1982; Crowder and Magnuson 1983). Some studies of fish temperature preference have suggested that food influences the long-term temperature preference of fish in the direction of energetic maximization (Javaid and Anderson 1967; Stuntz and Magnuson 1976; Reynolds and Casterlin 1979; Mac 1985), but the results are inconsistent and equivocal. Field studies, other than Brett's (1971), have also suggested that the combination of food and temperature may be the major influence on the distributions of fish observed in lakes (Caulton 1978; Rudstam and Magnuson 1985; Wurtsbaugh and Neverman 1988). Similar observations on the effect of food on temperature preference have been made for other ectotherms, such as reptiles and amphibians (Carey 1978; Porter and Tracy 1983).

The preliminary evidence that fish may integrate the effects of food and temperature led Crowder and Magnuson (1983) to propose the behavioral energetics hypothesis. This states that a fish should selectively choose the habitat with the highest net energetic value (i.e. highest surplus power (Ware 1982)) relative to other habitats. The energetic value of a habitat is determined by the integration of food and temperature using the fish bioenergetics model (Kitchell et al. 1977). The hypothesis also suggests that energy conservation measures such as moving to cooler temperatures during non-feeding periods might be employed (Ware 1982). Huey and Slatkin (1976) suggested a similar cost-benefit analysis of environmental factors and their joint effect on behavior of lizards, and Porter and Tracy (1983) used this approach to predict limits on the distributions of terrestrial ectotherms.

The behavioral energetics hypothesis seeks to unify the previous theory on foraging and thermoregulation. Optimal foraging predicts habitat choice based on food alone; behavioral thermoregulation has a similar dependence on temperature. Behavioral energetics proposes that organisms integrate the effects of food and temperature in choosing habitats. The separate predictions of these three hypotheses will be the same in some cases, but the question here is which hypothesis best describes non-overlapping cases? The purpose of this study was a simultaneous test of three alternative hypotheses (optimal foraging, behavioral thermoregulation, or behavioral energetics) for predicting short-term patch choice of bluegill when both food and temperature are manipulated.

TABLE 1. Food–temperature options for each patch choice experiment. The percentages represent the portion of maximum daily ration (Cmax) that was delivered on opposite tank sides during an experiment. Indicated temperatures were maintained within +/− 0.1°C. In experiments 2 and 3, the two food–temperature combinations noted for each experiment were tested simultaneously, four fish for each food–temperature combination (as opposed to eight fish for the food–temperature combinations tested in experiments 1 and 4).

Experiment number	Treatment
1	50% Cmax at 30°C vs. 50% Cmax at 25°C
2	25% Cmax at 30°C vs. 25% Cmax at 25°C
2	25% Cmax at 30°C vs. 75% Cmax at 25°C
3	12.5% Cmax at 30°C vs. 12.5% Cmax at 25°C
3	12.5% Cmax at 30°C vs. 75% Cmax at 25°C
4	50% Cmax at 30°C vs. 50% Cmax at 28°C

Materials and Methods

We conducted experiments using 8–12 g bluegill (60–70 mm total length) in a shuttle tank system in which individual fish could choose between different combinations of temperature and food availability. Eight shuttle tanks, designed after Neill et al. (1972), were placed in an isolation room equipped with fluorescent lights set on a 12:12 h light:dark cycle (light from 0700–1900). The fish had access to the two sides of a shuttle tank through a small tunnel (PVC tube 36 mm ID and 60 mm long). Each side of a shuttle tank was equipped with a computer-operated feeder (Gerbrands model G5110) which delivered 20-mg fish pellets which had a caloric density of 4200 cal/g (P. J. Noyes Inc.). The fish had about 3 s in which to capture a pellet as it dropped through the water column before it entered a collecting funnel and bottle. Temperature on each side of a tank was regulated through the combined use of a thermistor (YSI 44034), to measure temperature, and a submersible heater which was automatically controlled. The water in each side of the tank was mixed and oxygenated by an airstone. Cover was supplied by an overturned clay pot with a small entrance hole near the top. The entire system was continuously controlled and monitored by computers (Cyborg ISAAC 2000 linked to an IBM PC). This allowed us to collect a time series of fish location and temperature data for all the shuttle tanks simultaneously. Additional details of the experimental system are available in Wildhaber and Crowder (1991).

Bluegill sunfish were seined from local ponds and held in the laboratory (fed on pelleted food) at 25 ± 2°C for at least 2 wk prior to use (final preferred temperature for bluegills is 30°C, Neill and Magnuson 1974; Coutant 1977). Before we began any experiments, the maximum daily ration (Cmax) of a 10-g bluegill feeding on 20-mg pellets was estimated (Cmax = 24, 20 mg pellets) so that we could calibrate the food treatments. The experimental design used in the food × temperature experiments was a crossover (Gill 1978) with treatments (the combinations of food availability and temperature on each side of the tank — i.e. patch) continued long enough (7–12 d) to allow fish response to stabilize and then reversed relative to the two tank sides for another 7 d.

By using the crossover design, changes in behavior of individual fish over time could be assessed and controlled. The

main assumption of the crossover design is that residual effects from the first period to the second are minimal. For the two major response variables, patch usage (mean proportion of time spent on a tank side) and activity (mean number of tank position changes made per hour), residual effects were minimized by analyzing only the mean response from the last 3 d of each week for each fish. In experiment 3 (Table 1), the second experimental period is represented by the data from day 4 alone because on day 5 a system malfunction prevented further data collection.

We performed a series of experiments to describe how bluegill respond to food availability and temperature combinations. Four experiments were done over an 8 mo period (Table 1). In the initial experiment (50% Cmax at 30°C vs. 50% Cmax at 25°C), there were three possible outcomes, each associated with one of the three hypotheses under consideration: (1) No difference in usage between tank sides because food was equal (optimal foraging); (2) Usage greatest for the tank side at 30°C (behavioral thermoregulation); (3) Usage greatest for the tank side at 25°C (behavioral energetics). Based on bluegill bioenergetics model simulations, 50% Cmax at 25°C should produce a higher daily growth rate than 50% Cmax at 30°C. The other three experiments were performed to help clarify the relationship between food and temperature that we observed in the first experiment. In particular, we conducted experiments where four fish were tested at low food availabilities and four were tested with additional food available at 25°C, simultaneously (Experiments 2, 3). We also conducted experiments with a smaller, but still energetically important temperature difference between patches (Experiment 4).

For each experiment, naive bluegill were taken from the 25 ± 2°C holding tank and placed in an unpartitioned 76-L aquarium, temperature held at 25 ± 0.5°C (28 ± 0.5°C for experiment 4), within the isolation room. We presented these bluegill with food availability levels equal to our estimate of their Cmax over a 10-h period (0800–1800) for 2 d to familiarize them with the pellet delivery system. These bluegill were then held in the same tank for 24 h without food, weighed, and one was placed in each shuttle tank on the 25°C (or 28°C for experiment 4) tank side. Only one fish was used in each tank to avoid agonistic social behavior (Beitinger and Magnuson 1975; Medvick et al. 1981). We then gave the fish free access to both sides of their shuttle tank for 48 h without feeding to allow them to adjust to the shuttle tank.

For each experiment, eight naive bluegill were used. For experiment 4, data from only seven fish were used in the analyses due to a feeder malfunction in one tank that was not discovered until the end of the experiment. This individual was included in the growth analysis because we concluded that the malfunction did not compromise the growth data. Thus, these four experiments represent the results from 32 individual fish. During each experiment the sides of each tank were kept within ±0.1°C of the designated temperature.

The computerized pellet delivery system made food available from 0800 to 1000 each morning; actual pellet delivery times were randomized each day. Daily, the isolation room was opened after 1100, to allow for tank cleaning, and closed by 1400. Except for this maintenance period, we continuously monitored fish activity and tank side usage. In this paper we refer to data from four time periods: light, prefeeding (0700–0800); light, feeding (0800–1000); light, postfeeding (1500–1900); and darkness (1900–700). After the last day of feeding, we again witheld food for 24 h before a final weight was taken for each individual fish.

TABLE 2. *P*-values for ANOVA of mean tank side usage. These analyses were done on the mean value for the last 3 d of each experimental period for each time period (Feeding = 0800–1000, Prefeeding = 0700–0800, Postfeeding = 1500–1900, Darkness = 1900–0700) within an experiment. NS stands for not significant at the $P<0.05$ level and — stands for not applicable.

Independent variable	$P <$ Value for experiment number 1	2	3	4
Higher temperature				
Feeding	0.0001	0.025	NS	NS
Prefeeding	0.0001	0.003	0.003	0.025
Postfeeding	0.0001	0.0001	0.0001	0.025
Darkness	0.0001	0.025	0.005	NS
Time period *X* Temperature	0.0001	0.01	0.002	NS
Time period *X* Temperature *X* Higher food	—	0.005	NS	—

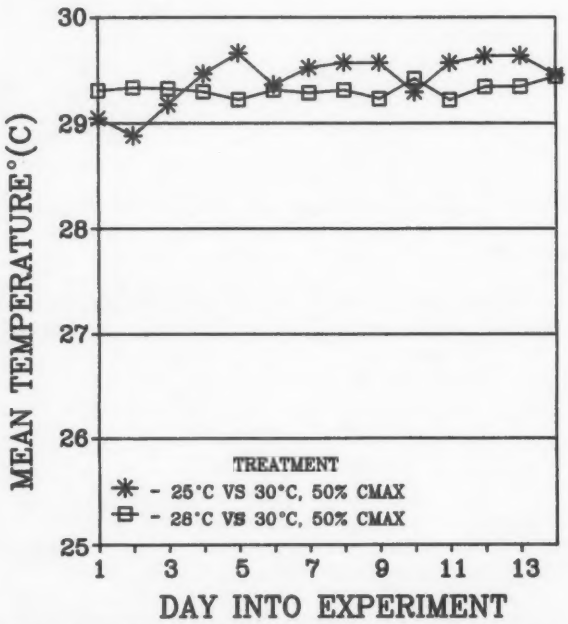

FIG. 1. Mean daily temperature experience for all the fish in an experiment which were exposed to equal food levels (50% Cmax) on both sides of a tank. The two lines represent temperature choice combinations of 25°C vs. 30°C and 28°C vs. 30°C. Day 8 is the first day that temperatures for the two sides of a tank were reversed.

We analyzed the data using crossover design analysis of variance (in experiments 2 and 3, the feeding treatment was one of the blocking factors). Tank side usage and activity were analyzed separately for each of the four time periods (0700–0800, 0800–1000, 1500–1900, and 1900–0700), and in a split-plot design with time periods as the subplots to assess differences in responses within and among time periods.

To get a direct estimate of the effects of the different food availability and temperature level combinations on bluegill growth, we also carried out a 2-wk growth experiment using

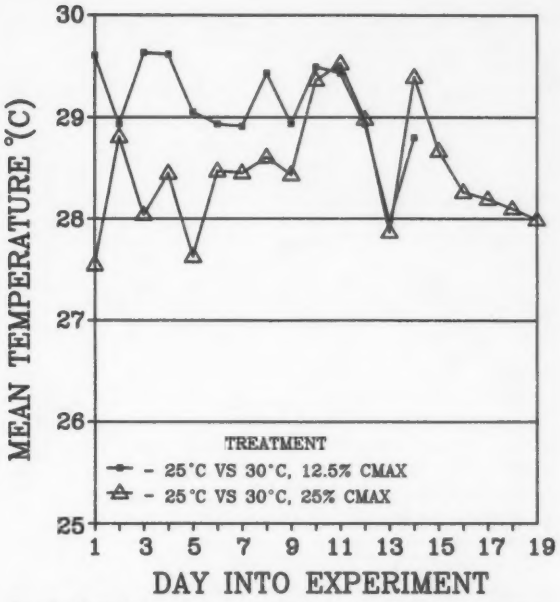

FIG. 2. Mean daily temperature experience for all the fish in an experiment which were exposed to equal food levels (12.5% Cmax or 25% Cmax, one line for each food availability level) on both sides of a tank. For food availabilities of 12.5% Cmax and 25% Cmax, day 11 and day 13, respectively, are the first days that temperatures for the two sides of a tank were reversed.

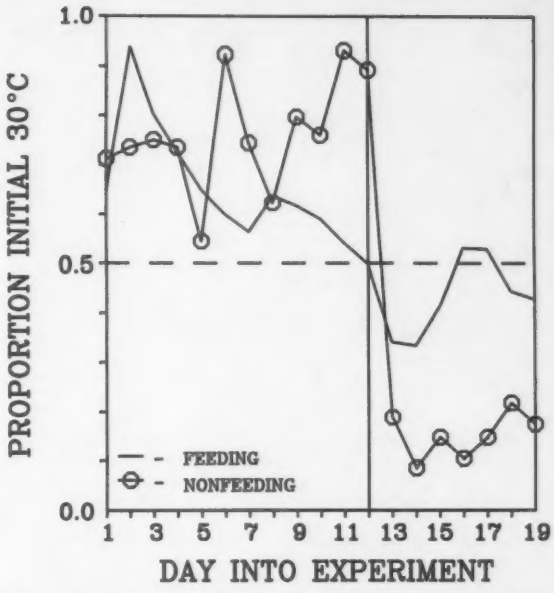

FIG. 3. Mean daily proportion of time spent on the initially warm side of a tank for fish where food was 75% Cmax on the 25°C side of a tank and 25% Cmax on the 30°C side. Nonfeeding and feeding periods are graphed separately. Day 13 is the first day that temperatures for the two sides of tank were reversed.

16 naive bluegill. Two food availability levels, one the lowest (12.5% Cmax) and one the highest (50% Cmax) used in the patch choice experiments, were both tested at 25°C and at 30°C. As in the patch choice experiments, growth rates were determined by the differences in initial and final wet weights of the fish. In this experiment, we used the same size bluegill, the same pelleted food, and the same protocol that were used in the patch choice experiments. The only difference between this growth experiment and the patch choice experiments was that the bluegill were confined to only one side of a tank. Along with data from this growth experiment, we have growth data from eight other buegill that were tested at the same food availabilities. These data are from preliminary growth experiments where the fish were introduced to a test tank from a community tank kept at 30°C.

Results

Bluegill generally spent more time on the 30°C side of the tank during both feeding and non-feeding time periods (Table 2, for the feeding period in experiment 3; $P<0.1$; in experiment 4, $P<0.08$); there were no significant differences among individual fish during any time period. Higher usage of the 30°C tank side was clear in all of the experiments; mean temperatures occupied throughout the day favored the warmer temperature (Fig. 1, 2). In experiments 2 and 3, half of the bluegill were given equal food on both sides of a tank and half were given much higher food on the cooler (i.e. 25°C) tank side. During the feeding period in these experiments, bluegill spent more time on the 25°C side when there was also higher food than they did when food levels on the two sides were equal

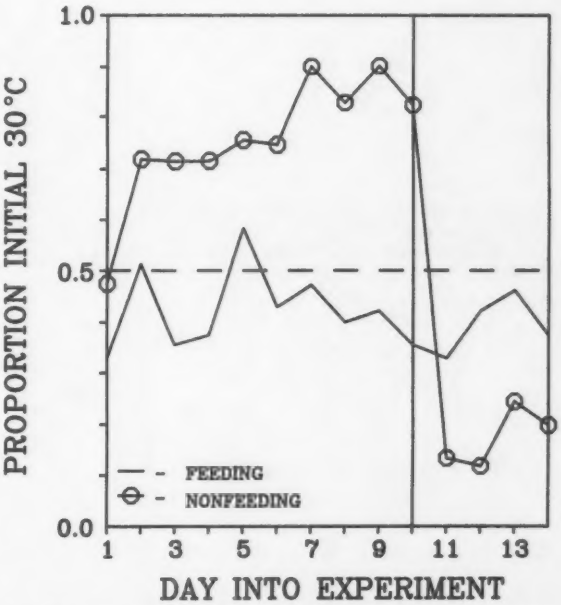

FIG. 4. Mean daily proportion of time spent on the initially warm side of a tank for fish where food was 75% Cmax on the 25°C side of a tank and 12.5% Cmax on the 30°C side. Nonfeeding and feeding periods are graphed separately. Day 11 is the first day that temperatures for the two sides of tank were reversed.

TABLE 3. *P*-values for ANOVA of mean activity per hour. These are the results from the analyses done on the mean value from the last 3 d of each experimental period for each time period (Feeding = 0800–1000, Prefeeding = 0700–0800, Postfeeding = 1500–1900, Darkness = 1900–0700) within an experiment. NS stands for not significant at the $P<0.05$ level and – stands for not applicable.

Independent variable	$P <$ Value for experiment number 1	2	3	4
Individual				
Feeding	NS	—	—	0.004
Prefeeding	NS	—	—	0.025
Postfeeding	NS	—	—	NS
Darkness	NS	—	—	NS
Time period	0.001	0.0001	0.0001	0.0001
Time period X Higher food	—	NS	0.025	—

TABLE 4. Mean growth (grams wet weight) of bluegill during 2-wk growth experiment at different temperatures and food availability combinations. SE stands for standard error.

Food availability % Cmax	Temperature (C)	Number of fish	Average growth (g)
12.5	25	4	0.19 (SE = 0.07)
12.5	30	4	0.04 (SE = 0.11)
50	25	4	1.70 (SE = 0.09)
50	30	4	1.34 (SE = 0.10)

($P<0.06$ and $P<0.1$ for experiments 2 and 3, respectively). There was no evidence of a preference for higher food patches when they were associated with cooler temperatures (Fig. 3, 4); bluegill show strong preferences for higher food when temperatures are equal (Wildhaber 1989). In all but experiment 4, bluegill spent significantly more time on the 30°C side of the tank during nonfeeding than feeding periods (Table 2, e.g. Fig. 3, 4). Thus, the behavioral thermoregulation hypothesis is a better predictor of the observed behavior of the bluegill in this study than either the optimal foraging on behavioral energetics hypotheses.

In all of the experiments, activity (number of tunnel passes per hour) differed among time periods (Table 3). The trend was increased activity going from darkness to postfeeding to prefeeding to feeding. The range in mean activity per hour, averaged over individuals and experimental periods, among experiments, was 1.0–2.7 moves per hour for 1900–0700 vs. 51.9–61.6 moves per hour for 800–1000. There were no significant differences in this activity pattern among individual fish. In experiments 2 and 3, there was no significant difference in activity among those bluegill with a low food availability on both sides of a tank and those bluegill which had a higher food availability choice in cold temperatures.

Growth

Our expectations from the bluegill bioenergetics model were that the fish could have gained more weight by choosing cooler temperatures at which to feed, or, in particular, by choosing cooler temperatures during non-feeding periods. Our growth data (Table 4) indicates that bluegill given limited food grew better at cooler temperatures. At 12.5% Cmax, growth was significantly better at 25°C than at 30°C whether we used all the growth observations or only the four for each food availability

TABLE 5. Growth data (grams wet weight) or each food–temperature combination in the patch choice experiments. Percentages represent the portion of maximum daily (Cmax) that was delivered on opposite tank sides during an experiment. SE stands for standard error and — stands for unavailable masses.

Food–temperature combination	Number of fish	Mean growth (g)
50% (30°C) vs. 50% (25°C) Cmax	8	1.01 (SE = 0.14)
25% (30°C) vs. 25% (25°C) Cmax	4	0.55 (SE = 0.10)
25% (30°C) vs. 75% (25°C) Cmax	4	1.57 (SE = 0.22)
12.5% (30°C) vs. 12.5% (25°C) Cmax	4	—
12.5% (30°C) vs. 75% (25°C) Cmax	4	1.45 (SE = 0.45)
50% (30°C) vs. 50% (28°C) Cmax	8	1.29 (SE = 0.11)

by temperature combination from the growth experiment ($P<0.001$ or $P<0.05$, respectively). At 30°C and 12.5% Cmax bluegill on average lost weight (i.e. mean growth was −0.42 g); only two of the 10 bluegill showed positive growth. In all the other food availability by temperature combinations no bluegill lost weight. At 50% Cmax bluegill also grew better at cooler temperatures ($P<0.001$).

The behavioral energetics hypothesis (Crowder and Magnuson 1983) and the observed growth rates of bluegill at different food availabilities and temperatures (Table 4) both predicted short-term bluegill behavior opposite of what was observed. We expected a decline in mean temperature occupied at lower food availabilities, but the only observed decrease in occupancy of the warmer patch occurred during feeding, especially when food was more abundant in the cooler patch (Fig. 3, 4; Table 2) and under food availabilities where growth was near zero or negative. At low food availabilities (i.e. 25% Cmax vs. 25% Cmax, experiment 2 and 12.5% Cmax vs. 12.5% Cmax, experiment 3), the mean temperature experienced during an experiment was lower than those experienced at higher food availabilities (50% Cmax vs. 50% Cmax, experiment 1). Mean bluegill temperature experience for experiments 1, 2, and 3, at the food availabilities that were equal for the two tank sides, were 29.4°C, 28.5°C, and 29.2°C, respectively ($P<0.001$ for experiment 1 vs. experiment 2).

A comparison of the growth rates observed in the growth experiment (Table 4, food availability of 50% Cmax) and that of experiment 1 (Table 5) shows that bluegill shuttling between temperatures grew less well than bluegill held at a constant 30°C ($P<0.001$) or 25°C ($P<0.0005$). This occurred even though bluegill which shuttled between temperatures had a lower mean temperature experience than bluegill held at a constant 30°C. In fact, bluegill at 50% Cmax, that had to shuttle across a 5°C gradient (experiment 1 where overall mean number of position changes per hour was 12.1) grew less well than bluegill that had to shuttle across a 2°C gradient (experiment 4 where the overall mean number of position changes per hour was 13.2) ($P<0.0005$, $n=8$, and $P<0.1$, $n=7$, Table 5); this suggests effects on behavior due to unaccounted-for costs of rapid moves between extreme temperatures.

Discussion

When food and temperature both vary, behavioral thermoregulation is a better predictor of short-term (minutes to weeks) habitat choice by bluegill than optimal foraging or behavioral energetics. The implication is that short-term habitat choice is not based on the bioenergetic integration of food and temper-

ature as described by current bioenergetic models. Rather, the decision appears to be a hierarchical one; temperature appears to be more important than food.

This is not to say that food does not affect habitat choice, such behavior has often been documented (Pyke 1984). Wildhaber and Crowder (1991) demonstrated that bluegill are able to respond to differences in food availability between patches as small as 25%. In the experiments reported here, bluegill activity patterns were influenced by food, even in the presence of a temperature gradient. The temperature-food hierarchy may be based on spatial properties of aquatic systems.

Temperature seems to be in the realm of macrohabitat choice for bluegill; moving from one thermal habitat to another may involve exposure to a completely different food resource/predator field. Within these temperature macrohabitats, food may be patchily distributed and thus, may influence microhabitat choice of bluegill. Bluegill respond rapidly to temperature and are sensitive to small temperature differences (Beitinger 1977; Neill and Magnuson 1974; Stuntz and Magnuson 1976). Thus, based on sensitivity, temperature would generally be of more immediate importance than food. When extreme differences in food levels between patches occur, bluegill will partially adjust their temperature–patch choice, temporarily, in order to exploit those differences in food.

At constant temperatures, bluegill differentially use patches with higher food (Wildhaber and Crowder 1991) and allocation of time to patches is similar to that predicted by matching theory. Matching theory predicts that the proportion of time spent in a patch will be the same as the proportional value of the patch relative to the overall food value of the environment. Using matching theory to predict patch use, based on food alone, the predicted use of the high food patch in experiments 2 and 3 would be 75% and 86%, respectively; we observed 46% and 49%. This strongly suggests that temperature can override patch use based on food alone.

In the short term, bluegill do not appear to assess the overall energetic value of a patch and choose the patch with the higher net energetic value. Rather, bluegill maintain their body temperature as close as possible to their final preferred temperature of 30°C, even at intermediate and low food availabilities when they would grow better at the available temperature of 25°C. Once foraging is completed, bluegill spend most of their time at temperatures near their final preferred temperature. This is surprising because estimated energetic costs of staying at 30°C rather than at 25°C during non-feeding periods are equivalent to a reduced growth rate of about 0.8% of body weight per day (Crowder and Magnuson 1983). Fish in natural systems sometimes enter cooler than the preferred temperatures to forage and then return to warmer temperatures when not foraging (Neill and Magnuson 1974; Wurtsbaugh and Neverman 1988). Also, bluegill have been observed to temporarily enter lethally warm temperatures to obtain food when food was not available at the final preferred temperature (Neill and Magnuson 1974).

When bluegill were held at or below maintenance rations, they compensated somewhat by occupying cooler mean temperatures. This decrease in mean daily temperature was less than 1°C over a 19 d experiment. For bluegill at rations equal to the lowest two food availabilities we offered, the behavioral energetics hypothesis predicts reductions in preferred temperature of 10°C or more below the final preferred temperature if such temperatures are available (Crowder and Magnuson 1983). In all of our experiments, we expected bluegill to spend most of their time in the cooler of the two available temperatures, especially when food availability was low.

What prevents bluegill from choosing habitats based on what appears to be the best way to maximize growth and thus presumably fitness? For fish and other ectotherms, body temperature changes with changes in environmental temperatures. Although body temperature may rapidly change with environmental temperatures, the physiological status of ectotherms changes much more slowly (i.e. acclimation must still occur, Fry 1971). Acclimation requires many physiological changes in fish such as in membrane fluditiy (Cossins and Posser 1978), in acid–base balance and ion fluxes (Crawshaw 1979), in thyroid function (Grau 1988), and in the function of enzyme systems (Somero 1969; Shaklee et al. 1977). The result is that the process of acclimation may require days to weeks (Brett 1956; Cossins et al. 1977). For the short-term habitat choice changes predicted by the behavioral energetics hypothesis to be effective in enhancing growth, acclimation would have to take place over a time span of minutes to hours.

Many physiological changes necessary for complete acclimation to new temperatures progress at a faster rate when new temperatures are higher, as opposed to lower, than the current temperature (Brett 1956; Otto and Rice 1974; Cossins et al. 1977; Hutchinson and Maness 1979). Overall, acclimation to colder temperatures may take weeks as opposed to a day for acclimation to warmer temperatures (Brett 1956; Cossins et al. 1977). The slower rate of acclimation to colder temperatures than warmer temperatures is probably due to the exponential rates of physiological processes (Brett 1956; DeWitt and Friedman 1979, e.g. membrane adjustments, Cossins et al. 1977).

Under an exponential model, in the process of reaching acclimation to new temperatures, acclimation to colder temperatures slows while acclimation to warmer temperatures speeds up. These arguments may also explain the much smaller than expected magnitude of the decline in mean temperature occupied by our fish under restricted food availabilities, Our study, and previous studies of temperature preference of fish on restricted rations (Javaid and Anderson 1967; Stuntz and Magnuson 1976), may have been too short to see the full extent of the downward adjustment in temperature preference that may occur. We have no data to support the kind of short-term shifts in thermal preferences, as a function of feeding, reported by Reynolds and Casterlin 1979). Their data on two bluegill show day-to-day declines in temperature preference with starvation and increases with feeding. Our data on 32 fish show strong, sustained preferences for 30°C. The reasons for this conflict remain enigmatic.

In our experiments and those of others on the effects of ration level on temperature preference in fish, one general pattern emerges. When fish are introduced to the experimental system they immediately increase their temperature preference to temperatures near the final preferred temperature for the species despite previous acclimation temperatures (Beitinger and Magnuson 1976; Stuntz and Magnuson 1976; Reynolds and Casterlin 1979; this study). The expected and observed results were poorer growth at these warmer temperatures than these bluegill were already experiencing. The explanation for such "odd" behavior seems to lie in the fact that most biochemical and physiological processes in ectotherms are optimal at or near a species final preferred temperature (Brett 1971; Dawson 1975; Beitinger and Fitzpatrick 1979; Hutchinson and Maness 1979). Bluegill appear to maximize physiological capacity first and then respond to ration level. The cost of this strategy seems to

be a limited potential for increased growth through decreased temperature preference.

Physiological constraints related to acclimation costs, not included in the standard bioenergetics model, appear to limit the bluegill's ability to respond rapidly to decreased rations by decreasing temperature preference. Why might fish evolve such a conservative strategy for dealing with their environment? Why do many temperate fish not possess different enzyme systems for cold and warm temperature which can be switched off and on as needed? The multiple isozyme systems of rainbow trout are a good example of such a mechanism (Hochachka and Somero 1984) which seems not to be present in the green sunfish (Shaklee et al. 1977), a close relative of bluegill.

The answers may lie in the environment in which bluegill have evolved. Generally water temperatures in littoral zone and surface water habitats occupied by bluegill are near their final preferred temperature during the growing season (Magnuson and Beitinger 1978). Correlated with this distribution of final preferred temperatures is a generally higher level of food availability and/or cover from predators (e.g. Mittelbach 1981, 1984, 1988). With such a strong correlation between food and temperature, it may be that bluegill never evolved the ability to integrate food and temperature at the short time (minutes to weeks) and space scales of our experiments. If a bluegill can choose patches based on temperature which are also good choices with respect to food, there is no need to develop a more complex and possibly more costly short-term choice mechanism.

In our experiments, bluegill only had to deal with two of the many factors they must respond to in natural systems. Each additional environmental factor added to the macrohabitat vs. microhabitat choice model we have suggested here must be assessed as to its relative importance. A good example would be predation risk. Spatially, temperature would again seem to define the macrohabitat, and patchily distributed predators may determine microhabitat choice within that macrohabitat. Temporally, predation risk would seem to be more important and able to override temperature preference more rapidly and effectively than food. Predation risk has already been shown to override habitat choice based on food in bluegill and other fishes (Werner and Mittelbach 1981; Werner et al. 1983; Abrahams and Dill 1989).

Whether or not the behavioral energetics hypothesis applies to other fishes has yet to be tested. The most widely cited case of hypothesized bioenergetic integration in fish is for the sockeye salmon, a cold-water species (Brett 1971), which feed at warm temperatures at night but move to cooler water during the day to digest their meal. Clark and Levy (1988) have challenged Brett's bioenergetics hypothesis in favor of a model based on predation risk. Several species of *Tilapia* also migrate inshore to warm water to feed and offshore to cooler water to digest with purported bioenergetic benefits (Caulton 1978). Another study of fish growth, under unrestricted ration, found highest growth rates when sculpin (*Cottus extensus*) were fed at low temperatures and digested food at high temperatures (Wurtsbaugh and Neverman 1988). The behavior observed by Wurtsbaugh and Neverman (1988) leads to higher energetic costs for maintenance, but confers a benefit of much higher daily rations and thus more rapid growth due to more rapid digestion.

If the behavioral energetics hypothesis can account for the behaviors of fish which move through a wide range of temperatures on a diel basis, it seems that a physiological mechanism such as an alternative isozyme system for cool and warm temperatures may be necessary. The previously noted acclimation costs might preclude anything less for such rapid changes in temperature to be energetically cost effective. Sockeye salmon may have such a system; a related species, rainbow trout, does have alternative isozyme systems (Hochachka and Somero 1984).

In conclusion, in the short-term (i.e. minutes to weeks), it seems that bluegill do not integrate the effects of food and temperature, as predicted by the behavioral energetics hypothesis. Some other costs, such as acclimation, which are not included in the model, may account for the disagreement between observed and predicted behaviors. In the long-term (i.e. seasonal), the physiology of bluegill can respond to food and temperature such that energetic gain (i.e. growth) is enhanced. But it is still uncertain whether, when long-term growth indicates better growth rates would be possible at lower temperatures, preference for lower temperatures may gradually replace the currently preferred temperature.

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Genetic Variation at the Malic Enzyme-2 Locus and Age at Maturity in Sea-run Atlantic Salmon (*Salmo salar*)

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Variation in the diallelic polymorphism at the malic enzyme-2 locus (Me-2) in Atlantic salmon is used extensively in descriptions of the population structure of this species. Genotypes at the Me-2 locus were examined in adult Atlantic salmon captured at the Girnock Burn, a tributary of the Aberdeenshire Dee, over 3 yr (1986–88), and in salmon caught in the commercial fishery in the estuary of the River Tay in 2 yr (1987–88). Initial observations on the Girnock Burn data suggested that Me-2 genotype frequency distributions differed between one-sea-winter fish (grilse) and multi-sea-winter fish (salmon) groups from the same hatch-year class. Data from the River Tay supported hypotheses constructed on the basis of the Girnock Burn data. Genotype frequencies in some grilse groups at both sites differed significantly from those expected under Hardy–Weinberg equilibrium, while those in salmon groups did not. The frequency of heterozygotes was generally significantly higher in grilse than in salmon from the same hatch-year class. The data suggest a variable association between Me-2 genotype and age at maturity, and a selective influence on the Me-2 locus. The implications of selective influences on this locus for estimates of gene flow among Atlantic salmon populations are discussed.

La variation du polymorphisme diallélique du locus de l'enzyme malique-2 (Me-2) chez le saumon de l'Atlantique est largement utilisée dans les descriptions de la composition de la population de cette espèce. Des génotypes du locus Me-2 ont été étudiés chez le saumon de l'Atlantique adulte capturé dans le Girnock Burn, un affluent de l'Aberdeenshire Dee, pendant une période de trois ans (1986–88), et chez les saumons capturés par la pêche commerciale dans l'estuaire de la rivière Tay pendant deux ans (1987–88). D'après les premières observations des données provenant du Girnock Burn, les distributions de fréquence du génotype Me-2 étaient différentes entre les poissons unibermarins (grilse) et les poissons pluribermarins (saumon) de la même classe d'éclosion. Les données de la rivière Tay appuyaient l'hypothèse formulée à partir des données du Girnock Burn. Les fréquences du génotype chez certains groupes de castillons (grilse) aux deux endroits différaient significativement des résultats prévus en vertu de l'équilibre de Hardy-Weinberg, tandis que celles des saumons ne différaient pas. La fréquence des hétérozygotes était en général beaucoup plus élevée chez les castillons que chez les saumons de la même classe d'éclosion. D'après les données, il semble qu'il y ait une association variable entre le génotype Me-2 et l'âge à la maturité, et une influence sélective sur le locus Me-2. Les répercussions des influences sélectives sur ce locus pour les estimations du flux génétique entre les populations de saumon de l'Atlantique font l'objet de discussions.

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Genetic protein variation is often assumed to be selectively neutral when applied to fisheries management (Allendorf and Phelps 1981). On this basis, high levels of genetic differentiation among populations have been regarded as evidence of a high degree of reproductive isolation in Atlantic salmon (Ståhl 1981; Koljonen 1989) and in other salmonids (Crozier and Ferguson 1986; Parkinson 1984; Wehrhahn and Powell 1987). However, it is possible for selection to maintain genetic differences among populations even in the presence of high levels of gene flow (Endler 1977).

Evidence of natural selection has been reported in a range of species and on a number of different traits, both mono- and polygenic (reviewed by Endler 1986). In fish species, there is evidence that some polymorphic protein loci are influenced by natural selection (Christiansen 1977; Henry and Ferguson 1985; Hines *et al.* 1983; Johnson 1971; Mitton and Koehn 1975; Place and Powers 1979). It is important to identify any loci at which variation is not selectively neutral in order to qualify the findings of studies of fish population structure based on assumed neutrality. Non-neutral loci can also be useful for studying the relationship between genotype, environment, and adaptation through natural selection.

A diallelic polymorphism at the malic enzyme-2 locus (Me-2) (E.C.1.1.1.40) in Atlantic salmon (*Salmo salar*) has

been reported to be present in populations across the species range (Cross and Healy 1983; Ståhl 1981; Verspoor 1988; Verspoor and Jordan 1989). The locus is expressed in the mitochondrial fraction of heart and skeletal muscle (Cross *et al.* 1979) and the genetic basis of the variation has been established by breeding studies (Johnson 1984). As one of the few commonly polymorphic protein loci so far identified in Atlantic salmon, allele frequency differences at the Me-2 locus can be expected to greatly influence measures of genetic differentiation among populations (Chakraborty and Leimar 1987). Recently Me-2 allele frequencies in salmon populations in both Europe and North America have been shown to be highly correlated with freshwater summer temperatures, suggesting that the polymorphism may be maintained by selective pressures (Verspoor and Jordan 1989).

This study was initiated after an observation on adult salmon captured in the fish trap on the Girnock Burn, a tributary of the Aberdeenshire Dee. In 1986, in the course of other work, it was discovered that 31 of the 38 grilse and 41 of the 77 multi-sea-winter salmon examined were heterozygous at the Me-2 locus. This suggested that differences might exist between Me-2 genotype frequencies in Atlantic salmon of different sea-age. The study was continued in subsequent years at the Girnock Burn to increase the power of tests on the initial observation and extended to the commercial fishery conducted on the estuary of the River Tay in Perthshire to test hypotheses generated on the basis of the Girnock Burn data.

Methods and Materials

Adult Atlantic salmon were captured in the Girnock Burn fish trap in October and November of 1986, 1987, or 1988. The fish were removed from the trap, anaesthetised with benzocaine, and a small muscle sample (~10 mg) was removed from the dorsal musculature using a 16 G diameter biopsy needle. Biopsies were also taken from fish captured in the commercial fishery in the estuary of the River Tay during the months of May–August in 1987 and 1988. Scales were taken from each fish.

Muscle samples were placed in plastic storage tubes with an approximately equal volume of 0.01 M Tris-HCl buffer (pH 7.4) and transported on solid CO_2 to the laboratory. Samples were stored at −60°C before being typed at the Me-2 locus using horizontal starch gel electrophoresis. The buffer system used was a continuous citrate-aminomorpholine system of Clayton and Tretiak (1972) adjusted to pH 6.6. Specific staining for malic enzyme was achieved using the procedure of Harris and Hopkinson (1976). The designation of malic enzyme loci and the nomenclature for the alleles present at the Me-2 locus follow Ståhl (1987). Genotypes at the Me-2 locus were unambiguously identifiable from the staining patterns observed.

Age determinations for each fish were made from the scales. Age nomenclature follows that of the Atlantic Salmon Scale Reading Workshop (Anon. 1984). The first digit in the age term shows the number of winters spent in freshwater, the second shows the number of winters spent at sea. A third digit in the age term indicates that the fish is a repeat spawner and shows the number of winters elapsing between the first and second maturations. In some fish no complete age record was evident from the scales taken. These fish were not considered further. None of the remaining fish were captured more than once. These were classified on the basis of freshwater-age, sea-age, and Me-2 genotype. Fish were assigned to one of the three possible Me-2 genotypes — 100/100, 100/125, or 125/125.

Statistical Analysis

Allele frequencies for each age group within hatch-year classes were found by direct counting from observed genotype frequencies. Homogeneity of allele and genotype frequencies within and among hatch-year classes at each site was tested using *G*-tests with Williams correction for sample size (Sokal and Rohlf 1981). Goodness of fit of observed genotype frequencies to those expected under Hardy–Weinberg equilibrium was assessed using *G*-tests with one degree of freedom (Ferguson 1980). Expected equilibrium frequencies were calculated using the formulae of Levene (1949) to correct for sample numbers.

Specific hypotheses on the effect of sea-age on the frequency of heterozygotes were tested using logistic regression analysis (McCullagh and Nelder 1983). For this purpose frequencies for the 100/100 and 125/125 genotypes were pooled, producing two genotype groups — homozygotes and heterozygotes. A logistic model describing the relationship between the frequency of each genotype and the effect of sea-age was fitted to the data for each year-class at each site separately. The model was of the form

$$\log\left(\frac{p_s}{1-p_s}\right) = \alpha$$

$$\log\left(\frac{p_g}{1-p_g}\right) = \alpha + \beta$$

where

p_s = frequency of heterozygotes among multi-sea-winter salmon (s);

p_g = frequency of heterozygotes among grilse (g);

α = constant which measures the frequency of heterozygotes in multi-sea-winter salmon;

β = constant which measures the difference between the frequency of heterozygotes in multi-sea-winter salmon and in grilse.

The null hypothesis in each case was that the frequency of heterozygotes was unaffected by sea-age (H_0:$\beta = 0$). The significance of each β value was assessed by comparing the ratio of the β estimate to its standard error with that of a standard normal distribution.

Probabilities from independent tests of significance were combined according to the method described by Sokal and Rohlf (1981). Where P is the probability from each test, then $-2\Sigma \ln P$ is distributed as χ^2 with $2k$ degrees of freedom, where k is the number of separate tests and probabilities.

Results

Girnock Burn

After 3 yr of study (1986–88) at the Girnock Burn site, data were available on Me-2 genotypes in age-groups from seven hatch-year classes (Table 1). No significant heterogeneity of allele frequencies was found among age-groups within hatch-year classes (1982 $G = 1.96$, df = 2, $P = 0.375$; 1983 $G = 1.84$, df = 3, $P = 0.607$; 1984 $G = 2.54$, df = 2, $P = 0.281$), but there was heterogeneity among hatch-year classes ($G = 12.88$, df = 4, $P = 0.018$). Data on age-groups within hatch-year classes were therefore pooled to generate an allele frequency for each hatch-year. These allele frequencies were used to generate Hardy–

TABLE 1. Deviations of observed genotype numbers from those expected under Hardy–Weinberg equilibrium in samples from the Girnock Burn (1986–88). Expected numbers are given in brackets. Age nomenclature is described in the text.

Year of hatch	Year sampled	Age	Genotype			Deviation from Hardy–Weinberg	
			100/100	100/125	125/125	*G*	*P*
1979	1986	4.3	1	0	0	—	—
1980	1986	3.3	1	0	0	—	—
1981	1986	3.2	14	22	6	0.23	0.632
			(14.76)	(20.48)	(6.76)		
1982	1988	3.3	1	0	0	—	—
	1987	3.2	13	29	11	0.95	0.330
			(12.14)	(26.71)	(14.14)		
	1986	3.3	5	19	9	1.20	0.273
			(7.63)	(16.75)	(8.63)		
	1986	3.1	0	17	4	10.84***	0.001***
			(4.63)	(10.73)	(5.63)		
	Σ		19	65	24		
1983	1988	3.2	14	25	10	0.34	0.560
			(15.88)	(24.25)	(8.88)		
	1987	2.2	19	24	12	0.78	0.377
			(17.92)	(27.17)	(9.92)		
	1987	3.1	9	12	2	1.05	0.306
			(7.80)	(11.40)	(3.80)		
	1986	2.1	2	14	1	6.29*	0.012*
			(5.76)	(8.48)	(2.76)		
	Σ		44	75	25		
1984	1988	2.2	10	13	4	0.63	0.427
			(11.89)	(12.23)	(2.89)		
	1988	3.1	6	9	2	0.22	0.639
			(7.00)	(8.00)	(2.00)		
	1987	2.1	10	6	1	1.85	0.174
			(7.00)	(8.00)	(2.00)		
	Σ		26	28	7		
1985	1988	2.1	10	14	2	0.77	0.380
			(11.00)	(12.00)	(3.00)		

Weinberg expected frequencies against which observed genotype frequencies in individual age-groups were tested. Although data from three-sea-winter fish (Table 1) were used when appropriate to calculate allele frequencies from pooled data, tests of deviation from equilibrium were not carried out on these groups due to their small size.

The deviations from equilibrium which were significant in the grilse groups sampled in 1986 remained so when compared to expected frequencies from pooled data (Table 1). However, there were no significant deviations from expected genotype frequencies in any of the four grilse groups sampled in subsequent years, and none in any salmon group sampled in any of the 3 yr of the study.

Combining probabilities from the separate tests of deviations from Hardy–Weinberg equilibrium showed that while genotype frequencies in salmon groups did not differ significantly from equilibrium frequencies ($\chi^2 = 10.55$, df = 12, $P = 0.568$), those in grilse groups did ($\chi^2 = 31.37$, df = 12, $P = 0.002$).

G-tests showed no significant heterogeneity of genotype frequencies between multi-sea-winter salmon age groups within each of the 1982, 1983, and 1984 hatch-year classes. In the same way, there was no heterogeneity between grilse age-groups within these hatch-year classes. Therefore data were pooled to produce a separate genotype frequency distribution for multi-sea-winter salmon and for grilse in each hatch-year class. The results of tests on homogeneity of these distributions (Table 2) showed a significant difference between genotype frequency distributions in salmon and grilse from the 1982 hatch-year class, and a difference with a probability of 0.067 between fish of the 1983 hatch-year class. The heterogeneity in genotype frequencies in the 1984 year class did not approach significance.

Logistic regression analysis allowed the testing of the effect of sea-age on the frequency of heterozygotes. In these tests the alternative hypothesis was that $\beta \neq 0$. The estimate and standard error of β for each hatch-year class were used to calculate an associated *t*-value and probability (Table 3). The pattern of results in these tests followed that of the tests on homogeneity of genotype frequencies. The value of β for the 1982 hatch-year class was significant and positive, indicating a higher frequency of heterozygotes among grilse than in multi-sea-winter salmon. In the 1983 hatch-year class there was a higher frequency of heterozygotes in grilse than in salmon but this was only marginally significant ($P = 0.056$). Sea-age had no significant effect on the frequency of heterozygotes in fish from the 1984 hatch-year class. The combined probability of the results from the tests on all three year-classes suggests an association between sea-age and the frequency of Me-2 heterozygotes ($\chi^2 = 12.89$, df = 6, $P = 0.045$).

On the basis of results from the Girnock Burn samples three hypotheses were constructed:
1) Me-2 genotype frequencies in grilse groups do not conform to Hardy-Weinberg equilibrium frequencies.
2) Me-2 genotype frequencies in salmon groups do conform to Hardy–Weinberg equilibrium.
3) There are more Me-2 heterozygotes among grilse than multi-sea-winter salmon of the same hatch-year class.

The corresponding null hypotheses were tested using data collected on the River Tay.

River Tay

Muscle samples were collected from fish at the River Tay site in 1987 and 1988 (Table 4). As at the Girnock Burn, there was no significant heterogeneity of allele frequencies among age groups within hatch-year classes (1983 $G=2.40$, df = 2, $P=0.301$; 1984 $G=3.05$, df = 2, $P=0.218$). Although there was no significant heterogeneity among hatch-years either ($G=1.25$, df = 3, $P=0.742$), data were pooled in the same manner as before to generate the genotype frequencies expected under Hardy–Weinberg equilibrium.

In two out of the four grilse groups there were significant deviations from expected equilibrium frequencies (age 3.1 from the 1983 hatch-year class and age 3.1 from the 1984 hatch-year class). Overall, the differences between observed and expected genotype frequencies in the four grilse groups were significant ($\chi^2=22.64$, df = 8, $P=0.004$), as predicted by the first of the three hypotheses. There were no significant departures from expectation in genotype frequencies in any of the single tests on two-sea-winter salmon groups (Table 4). Combining the probabilities from the single tests on salmon showed that there was no significant deviation from expectation overall ($\chi^2=9.56$, df = 8, $P=0.297$), as predicted by the second hypothesis.

The values of β from logistic regression analysis for each hatch-year class are shown in Table 5. In these cases the *t*-values were compared to one-tailed probabilities as the alternative hypothesis tested (Hypothesis 3: $\beta>0$) is directional. For both the 1983 and 1984 hatch-year classes the null hypothesis was rejected because the value of β was positive and significant, again indicating a greater frequency of heterozygotes among grilse groups compared to multi-sea-winter salmon.

Discussion

The hypotheses constructed on the basis of results from the Girnock Burn data are supported by the data from the River Tay. It appears, therefore, that genotype frequencies in grilse groups do not conform to Hardy–Weinberg equilibrium while those in multi-sea-winter salmon do. Additionally, it appears that there are more heterozygotes among grilse than among multi-sea-winter salmon.

Deviations from Hardy–Weinberg equilibrium, where they were significant in individual age-groups, occurred only in grilse and were characterised by an increase in the observed number of heterozygotes over expectation. These deviations were not restricted to a single site, a single hatch-year class at any site, or a single year of study. Tests of deviation of genotype frequencies from those expected under Hardy–Weinberg equilibrium are recognised to be insensitive. They are often misleading when used to imply the direction of selection in the absence of known zygotic or preselection genotype frequencies (Lewontin and Cockerham 1959). Even so, significant deviations from Hardy–Weinberg equilibrium were observed in a number of groups of grilse, indicating that some mechanism was acting to alter genotype frequencies. Although multiple *G*-tests were carried out on the data, the number of significant results, the levels of significance, and the fact that the direction of deviation was always the same suggest that these results were real and not statistical artifacts.

Endler (1986) suggests that deviations of genotype frequencies from Hardy–Weinberg equilibrium cannot be regarded as demonstration of selection as there are many assumptions implicit in the formal equilibrium model; no mutation, no migration among populations, random mating within populations, and no selection acting on the locus involved (Hartl 1980). Violation of any of these assumptions can affect genotype frequencies. Mutation rates at individual loci, estimated to be in the range $10^{-4}-10^{-6}$ per gamete (Ferguson 1980), are so low as to have a negligible effect on allele frequencies, and therefore on genotype frequencies, in studies of this type. It is unlikely that the results can be explained by migration or mating patterns which are the same over a number of years at two independent sites without implying fitness differences between genotypes. The consistency in the direction of deviation from Hardy–Weinberg equilibrium suggests that a deterministic rather than a stochastic mechanism underlies our findings. Moreover, any mechanism which affects genotype frequencies, other than selection, would be expected to affect the year-class as a whole and this was not the case. It is the differences in genotype frequencies between grilse and salmon

TABLE 2. Results of *G*-tests on homogeneity of genotype numbers in grilse and salmon groups from the Girnock Burn.

Year of hatch	Age at maturity	Genotype			*G*	Degrees of freedom	*P*
		100/100	100/125	125/125			
1982	Grilse	0	17	4	9.21	2	$P=0.010$
	Salmon	19	48	20			
1983	Grilse	11	28	3	5.40	2	$P=0.067$
	Salmon	33	49	22			
1984	Grilse	16	15	3	0.84	2	$P=0.658$
	Salmon	10	13	4			

TABLE 3. β values from logistic regression analysis on the effect of sea age on the Me-2 heterozygote frequency in groups of fish from the Girnock Burn.

	β			
Year-class	Estimate	Standard error	*t*-value	Probability
1982	1.239	0.596	2.08	0.034
1983	0.735	0.385	1.91	0.056
1984	−0.162	0.517	−0.31	0.757

from the same hatch-year which most strongly suggest a selective influence on the locus.

The differences were of variable magnitude in different hatch-year classes, but appeared significant overall at each site. Any environmental effect on fish of different genotypes might be expected to be of variable strength. The environmental conditions experienced by fish hatched in different years vary. Even within single hatch-year classes, fish remain in both freshwater and seawater for differing lengths of time. As a consequence, the conditions experienced by each life-history group from each hatch-year may vary markedly.

The available data suggest that heterozygosity at the Me-2 locus is associated with earlier maturation in adult salmon. Studies on rainbow trout (*Oncorhyncus mykiss*) have shown relationships between overall levels of heterozygosity at metabolic enzyme loci and components of fitness (Danzmann et al. 1988; Koljonen 1986; Leary et al. 1983). However, the association between earlier maturation and Me-2 genotype in salmon is significant in itself, suggesting a strong selective influence on this single locus.

The correlation between Me-2 allele frequency and summer freshwater temperatures (Verspoor and Jordan 1989), and a consistent increase in the frequency of the 125 allele in Scottish farmed salmon stocks when compared to their wild source populations (Youngson et al. 1989), suggest that directional selection can act on Me-2 allele frequencies. The findings of the present study suggest that balancing selection may also be a factor in the determination of Me-2 allele frequencies in natural populations.

From the results of this study, it cannot be determined whether selection is acting directly on the Me-2 locus or on some structurally linked or epistatic locus or loci. Mitochondrial malic enzymes show higher levels of activity in the muscle tissue of aquatic animals than in terrestrial animals, and Skorkowski (1988) has suggested that these enzymes may have a more prominent role in the metabolism of aquatic animals. If this is the case in Atlantic salmon, differences in the timing of the attainment of maturity may reflect kinetic differences between the Me-2 allozymes. Alternatively, it is possible that variation at the Me-2 locus is effectively neutral and acts only as a marker for a more extensive or chromosomal polymorphism, as found at the Pt-10 and the alpha-amylase loci in both *Drosophila pseudoobscura* and *D. persimilis* (Prakash and Lewontin 1968).

Of the loci routinely screened in studies on the population structure of Atlantic salmon, relatively few show widespread polymorphisms. Frequency differences in alleles at these loci

TABLE 4. Deviations of observed genotype numbers from those expected under Hardy–Weinberg equilibrium in samples from the River Tay (1987–88). Expected numbers are given in brackets.

Year of hatch	Year sampled	Age	Genotype			Deviation from Hardy–Weinberg	
			100/100	100/125	125/125	*G*	*P*
1980	1987	4.3	1	1	0	—	—
1981	1987	3.3	1	5	1	—	—
1982	1988	3.3	0	1	0	—	—
	1987	2.3	7	7	2	—	—
	1987	3.2	7	13	5	0.10	0.752
			(7.71)	(12.57)	(4.71)		
	Σ		14	21	7		
1983	1988	2.3	2	3	0	—	—
	1988	3.2	8	17	3	1.67	0.196
			(10.82)	(13.36)	(3.82)		
	1987	2.2	22	19	6	1.48	0.224
			(17.77)	(22.45)	(6.77)		
	1988	3.1.1	1	1	1	—	—
	1987	3.1	17	46	7	8.40**	0.004**
			(25.68)	(33.63)	(10.68)		
	Σ		50	86	17		
1984	1988	2.2	27	26	10	1.30	0.254
			(22.80)	(30.40)	(9.80)		
	1988	2.1.1	1	1	0	—	—
	1988	3.1	23	52	15	4.88*	0.027*
			(32.88)	(43.23)	(13.88)		
	1987	2.1	45	62	17	0.45	0.502
			(44.64)	(59.72)	(19.64)		
	Σ		96	141	42		
1985	1988	2.1	51	92	28	1.48	0.224
			(54.90)	(84.20)	(31.90)		

TABLE 5. β values from logistic regression analysis on the effect of sea age on the Me-2 heterozygote frequency in groups of fish from the River Tay. The probabilities cited are one-tailed probabilities.

	β			
Year-class	Estimate	Standard error	*t*-value	Probability
1983	0.642	0.331	1.94	0.026
1984	0.483	0.290	1.66	0.049

influence estimates of genetic differentiation among populations to a greater extent than frequency differences in rare alleles (Chakraborty and Leimar 1987). Previous measures of genetic differentiation in Atlantic salmon will have been determined to a major extent by allele frequency differences at the Me-2 locus and consequently may have been influenced by selection acting on the locus. Estimates of historical levels of gene flow in Atlantic salmon such as those produced by Ståhl (1981) and Koljonen (1989) using indices of fixation statistics developed by Wright (1943) may prove to be misleading, since this method assumes the selective neutrality of polymorphic loci (Slatkin 1985). Until it can be determined whether the selective forces on the Me-2 locus act to make allele frequencies more or less homogeneous, the scale and direction of any possible error in gene flow estimates cannot be assessed.

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Catchability Variations of Cod in the Marginal Ice Zone

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Fréchet, A. 1990. Catchability variations of cod in the marginal ice zone. Can. J. Fish. Aquat. Sci. 47: 1678–1683.

An analysis of results obtained during the winter groundfish surveys in the Gulf of St. Lawrence since 1978 was undertaken by relating the cod (*Gadus morhua*) catch to the distance from ice edge while taking temperature and depth variables into account. This analysis was prompted by anecdotal accounts and recently published data on increased abundance of many taxa related to an upwelling phenomenon in the marginal ice zone. Results indicate that large catches of cod occur in the marginal ice zone when depths are suitable. It is hypothesized that a strong thermal gradient close to the bottom would increase the concentration of cod and thus its catchability.

Une analyse des résultats obtenus lors de missions d'évaluation de poissons de fond dans le Golfe du Saint-Laurent en hiver depuis 1978 a été faite en reliant la capture de morue (*Gadus morhua*) à la distance de la marge des glaces tout en tenant compte de la température et de la profondeur. Cette analyse résulte d'informations anecdotiques ainsi que des données publiées récemment sur l'abondance accrue de plusieurs taxons dans la zone marginale des glaces causée par un phénomène de remontée d'eau profonde. Les résultats indiquent que les plus grosses captures de morue se retrouvent dans la zone marginale des glaces si la profondeur est adéquate. On pose l'hypothèse que la présence d'un fort gradient thermique près du fond pourrait causer une augmentation de la concentration de la morue et par le fait même sa capturabilité.

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Field observations of catch rates of fish during winter surveys indicate that very successful sets are encountered close to the ice edge. Templeman and May (1965) mention "... very large catches of post-spawning cod (*Gadus morhua*) were obtained on the southeastern slope (near Hamilton Inlet, Labrador) just south of the ice-edge at 225–280 m (2.8–3.0°C)." Chumakov and Savvatimsky (1990) have noted that Greenland halibut (*Reinhardtius hippoglossoides*) concentrations are found close to the ice edge in Baffin Bay at depths ranging from 500 to 1000 m.

Two cod stocks are present in the Gulf of St. Lawrence (3Pn, 4RS, and 4T-Vn [Jan.–Apr.]) and display similar migration patterns (Fig. 1). During the winter migrations of these stocks outside the Gulf into Subdivisions 3Pn and 4Vn (Jan.–Apr.), catch rates are high, almost twice those observed in September (Fréchet 1988).

Total biomass estimates of cod from the surveys conducted in winter show considerable inter-annual variation (Fréchet 1988). This apparently occurs because cod are densely aggregated in restricted areas, and the stratified random design of the survey does not adequately treat this type of distribution (Fréchet 1988). Although some of the variations may be attributable to changes in stock size, they may also be related to variations of catchability caused by a strong thermal gradient which induces concentrations of cod near the bottom and thus a larger availability to the trawl (Jean 1964; Forest and Minet 1981).

The purpose of this paper is to analyze to what extent catch rates of cod in the frontal ecosystem of the ice edge are higher than those observed in surrounding waters and if this might be a significant factor in the timing and extent of the winter migration of the 3Pn and 4RS cod stock. Temperature and depth are important factors influencing cod distribution (Jean 1964; Beverton and Lee 1965; Templeman and May 1965; Svetlov 1970) and will thus be taken into account.

Material and Methods

The Department of Fisheries and Oceans, Canada, has carried out nine annual winter groundfish trawling surveys aboard the research vessel *Gadus Atlantica* in the Gulf of St. Lawrence (NAFO Divisions 4RST and Subdivision 3Pn) from 1978 to 1987 (Fig. 1). These surveys were based on a depth stratified random selection of fishing stations (Doubleday and Rivard 1981). The area was surveyed by towing an Engel Hi-lift otter trawl at a speed of 3.5 knots for 30 min. Only sets done in Subdivision 3Pn and Divisions 4R and 4S were used in this analysis. Most surveys occurred in the month of January except for the 1980 and 1981 surveys which ended on February 11 and 17, respectively.

The distances separating the 1 374 sets to the ice edge were calculated by plotting the position of each set on a map of ice conditions in the Gulf of St. Lawrence. These maps were provided by the Atmospheric Environment Service of the Canadian Department of Environment and were compiled from a composite of information from ships of opportunity, aerial reconnaissance, satellite imagery, and shore observations. They were generally produced every third or fourth day and considered to be representative of the ice conditions at 1200 hr of the day of the report. A total of 64 maps were used to cover the surveys. To illustrate the variability in the location of the ice edge within the month of January, the surface of the Gulf covered by ice was calculated using an electronic planimeter (Tamaya digitizing area-line meter. Model:Planix 5000).

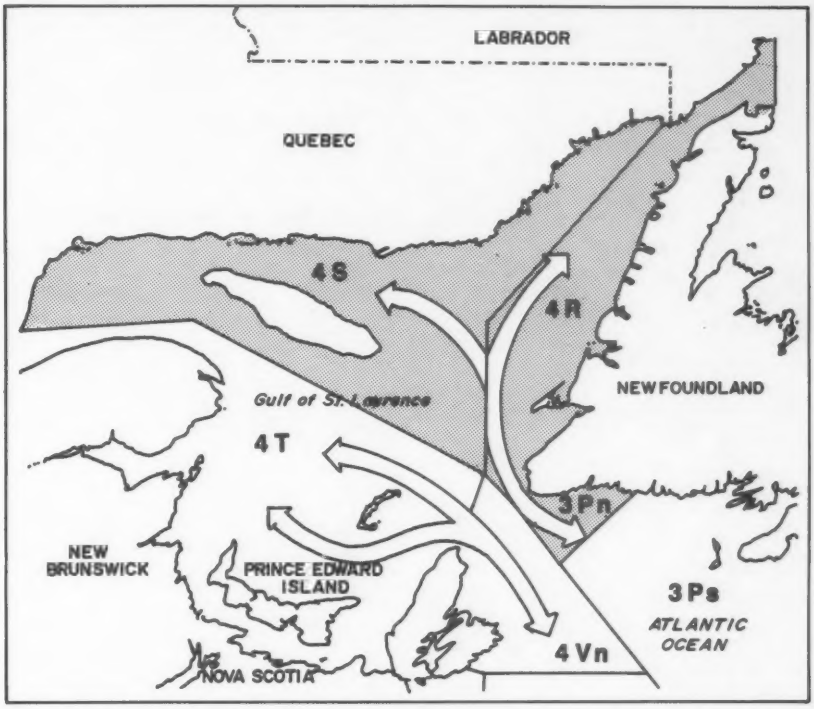

FIG. 1. NAFO Divisions and Subdivisions and migration routes of the two cod stocks (3Pn, 4RS and 4T,Vn [Jan. to Apr.]) in the Gulf of St. Lawrence. The study area is stippled.

TABLE 1. Partitioning of the strata, temperature, distance from the ice edge, and catch as input for the log-linear model.

Variable	Depth	Temperature	Distance[a]	Catch
Units	Fathoms	Celsius	Nautical miles	Kilograms
symbol	*Z*	*T*	*D*	*W*
grouping		(Quartiles)	(Quartiles)	(Quartiles)
Modality				
1	50,100	<3.9	<−15.1	<1.4
2	100,150	3.9,5.3	−15.0,8.5	1.5,13.5
3	150,200	5.3,5.9	8.6,44.0	13.6,105.3
4	>200	>5.9	>44.1	>105.4

[a]Negative values indicate fishing within the ice cover.

The position of individual sets was plotted on the map with the closest correspondence in time and the distance to the closest ice edge calculated irrespective of the ice concentration. The average change of the area covered by ice between successive maps was 12%. This means that the frequency of production of maps was sufficient to allow accurate positioning of sets relative to the ice edge.

The research surveys commenced in Subdivision 3Pn at maximum distance from the ice front. With time, sets were closer to the ice edge and eventually fishing operations occurred within the ice area. Distances separating all tows from the ice edge ranged from −100 to 200 nautical miles (a minus sign indicates that the set was done within the ice cover).

For every set, average depth trawled from echosunder traces (*Z*, in metres), bottom temperature from an expendable bathythermograph cast (*T*, in °C) distance from the ice edge (*D*, in nautical miles) and catch (*W*, in kilograms) of cod was recorded. These four variables were partitioned according to Legendre and Legendre (1983) to generate the multiway contingency table (Legendre 1987) for analysis using a log-linear model (Table 1). Temperature and catch were split by quartiles. Since the sampling design of groundfish surveys is based on depth strata with 50 fathom steps, this was maintained as a basis for delimiting depth intervals. In order to eliminate the possibility that a higher proportion of sets might have been made in the marginal ice zone (MIZ) (i.e. post stratification could bias the interpretation of the catch), the distance variable was also split into quartiles. As a result, the MIZ is considered to be equal to the third modality of the *D* variable (i.e. $D3 = 8.6$–44.0 nautical miles off the ice edge), this is consistent with the findings of Buckley et al. (1979) and Smith et al. (1985) of a homogeneous water mass. The origin and extent of the MIZ is likely to vary according to wind direction and speed, especially in the case of wind driven upwelling.

A multiway cross tabulation ($4\times4\times4\times4$) of the observed frequency of temperature (*T*), depth (*Z*), distance from ice edge (*D*), and catch (*W*) of cod was used in the log-linear analysis. This type of analysis was preferred because the catch variable showed a biological response curve that reached a maximum (or a minimum) for intermediate values of the environmental variables, temperature, depth, and distance from the ice edge (i.e. non-monotonic responses). Data were analyzed using the BMDP program P4F for portable computers. As certain cells were zeros, the log-linear parameters could not be calculated so a constant value of 0.5 (Delta) was added to the multidimensional matrix, as recommended (BMDP 1985).

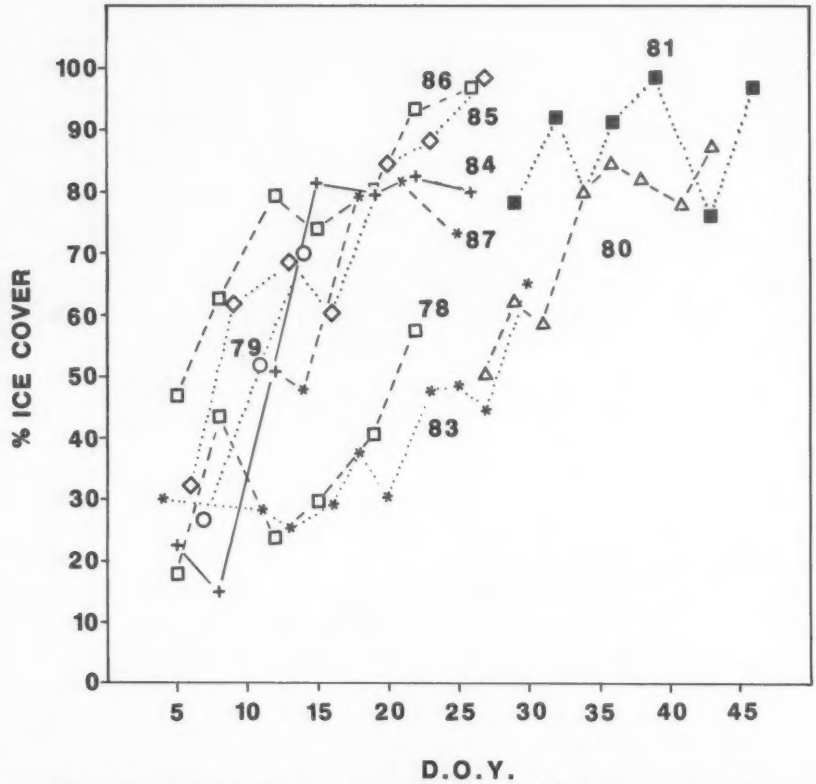

FIG. 2. Day of the year (D.O.Y.) of the area covered by ice in the Gulf of St. Lawrence for all surveys according to ice maps (Source: Atmospheric Environment Service of the Canadian Department of Environment).

Data were also analyzed by a multiple correspondence (Lebart et al. 1977). This analysis is used to compare various modalities of a variable (rows of a contingency table) to the modalities of a second variable (columns of a contingency table). In contrast to the log-linear analysis of multidimensional contingency tables used above, which identifies interactions between variables and not modalities, the correspondence analysis allows one to visualize how this interaction occurs. Statistical analysis was done using the SAS program SAS.BICORR from the public library of Laval University (Québec).

Results

Coverage of the Gulf by ice takes place during the month of January (Fig. 2). In most years, the survey commenced with only 20–30% ice cover and terminated with over 80%, and agrees with Markham (1980). This means that the ice edge location changes with time. Wind during sets originated mainly from the west and northwest, favorable to a progression of the ice cover from the Québec north shore towards Cabot Strait. In surveys since 1984, the progression of ice was rapid, 50% coverage being reached in all cases before the 11th of January (Fig. 2) and strong winds occurring frequently.

Yearly distribution of average catch per set to distance from ice edge show that large catches of cod are located at or close to the ice edge (Fig. 3). Although the complete range of distances was not sampled every year (especially in 1981), the modal category is often the ice edge. The average catch per set in the 1987 survey does not follow this pattern; most large catches were observed far from the ice edge. The biomass estimates from this survey were the lowest in the 9-yr time series and only small catches of cod were found in Subdivision 3Pn (Fréchet 1988). Since small concentrations of cod were observed that year, it is unlikely that the effect of the ice edge would be detected.

It is generally recognized that temperature and depth have an influence on cod distribution. The response curve is generally of a unimodal type. These two factors must thus be taken into account in the analysis of the effect of the ice edge to cod distribution. From these groundfish surveys, the largest catches of cod occurred in the 100–150 fathom range (Fig. 4a). As depth increased, the catch decreased. Large catches of cod were taken in water temperature in the 3.9–5.3°C range. Small catches dominated in sets done within the ice edge, whereas occurrences of large catches dominated in open waters (Fig. 4c).

Temperature, depth, and distance from the ice edge were expected to have an effect on cod catches so [*T*], [*Z*], and [*D*] were included in the log-linear model in order to explain the cod catches [*W*]. As log-linear models are hierarchical, an interaction is necessarily included with all its corresponding lower order effects. In this case, the starting model was:

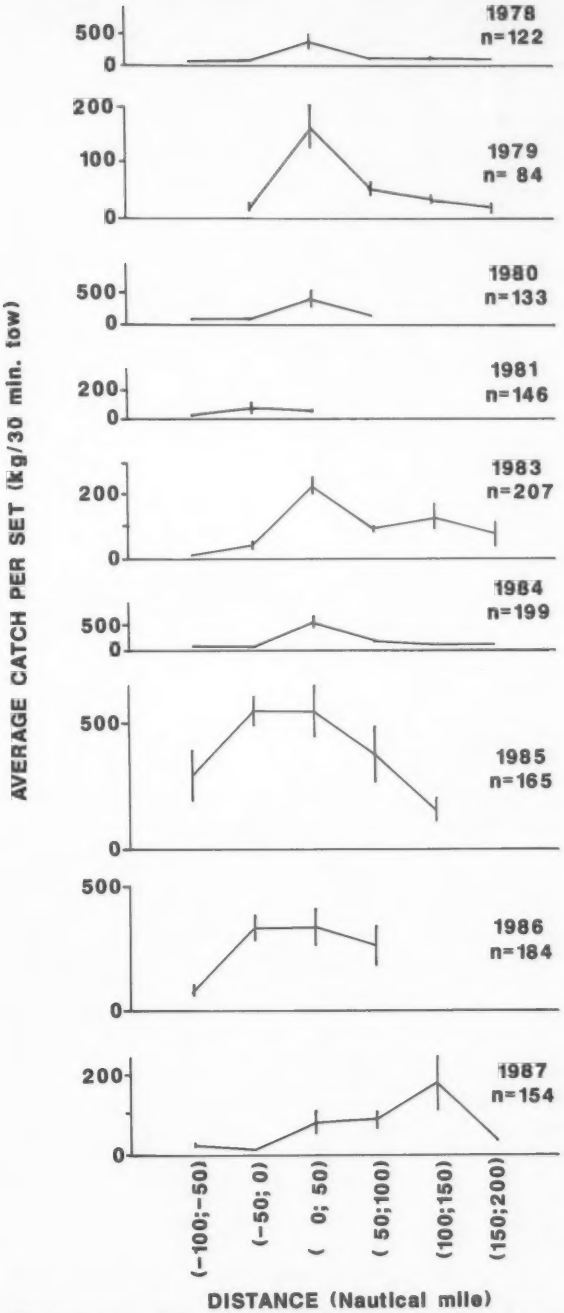

FIG. 3. Average catch of cod per fishing station (±1 s.d.) for every 50 nautical miles.

$$\ln(E) = [\phi] + [T] + [Z] + [D] + [W]$$

Where: E = expected cell frequency
ϕ = average of the logarithms of the expectations

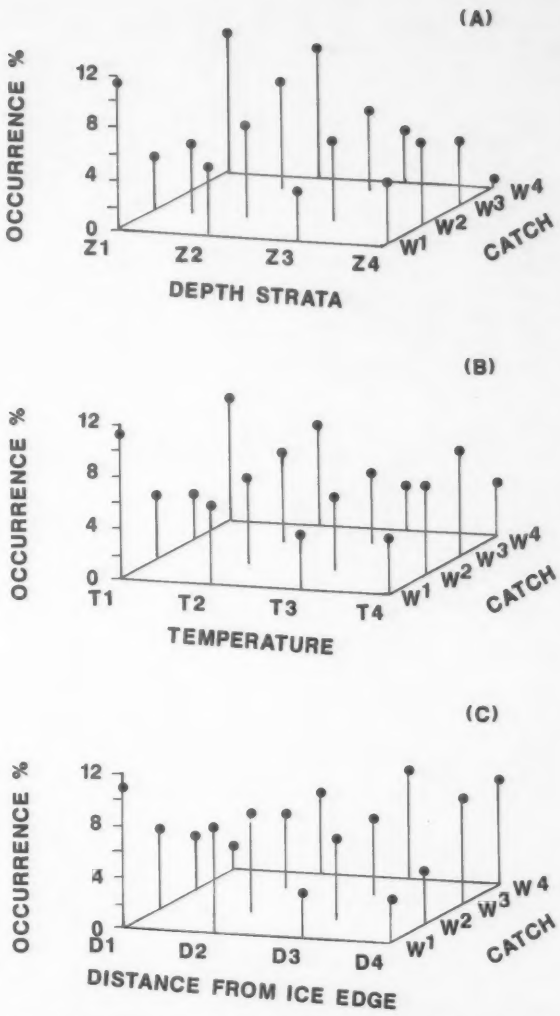

FIG. 4. Occurrence of catch categories according to depth (A), temperature (B), and distance from ice edge (C). See Table 1 for a description of modalities.

The depth/temperature was the most significant interaction from the multiway table, then the depth/catch and distance to ice edge/catch interactions were added to the model. Finally, with the addition of the catch/distance to ice edge/depth interaction, the model fitted the data ($P>0.01$) (Table 2). The catch/distance interaction was marginally less significant than the catch/depth interaction ($G^2=152$ compared to 177, df=9) which means that catch is slightly more related to the depth than the distance to the ice edge. The most parsimonious model is as follows:

$$\ln(E) = [\phi] + [T] + [Z] + [D] + [W] + [ZT] + [ZD] + [WZ] + [WD] + [WDZ]$$

The first two factors (or axes) explained 40% of the variance of all factors in the correspondence analysis (Table 3). Each modality of the four variables described in Table 3 are plotted

TABLE 2. Partitioning of the G^2 statistic, from the log-linear model. Effects included in the model are listed additively.

Model	df	G^2	Abbreviated model
[*W,D,Z,T*]	243	1485[a]	
Difference	9	758[a]	[*W,D,Z,T*]
+ [*ZT*]	234	727[a]	
Difference	9	177[a]	[*W,D,ZT*]
+ [*WZ*]	225	550[a]	
Difference	9	152[a]	[*D,WZ,ZT*]
+ [*WD*]	216	398[a]	
Difference	9	43[a]	[*WD,WZ,ZT*]
+ [*DZ*]	207	355[a]	
Difference	27	128[a]	[*DZ,WD,WZ,ZT*]
+ [*WDZ*]	180	227	[*WDZ,ZT*]

[a]$P <= 0.01$; G^2 correspond to models having a $P>0.01$ of fitting data.

TABLE 3. Relative contribution and explained variance (%) of the various modalities of the first two axes from the correspondence analysis. Symbols are those used in Fig. 5.

Variable	Symbol	Factor 1	Factor 2
Distance from ice edge	D1	0.2	23.7
	D2	0.0	0.7
	D3	0.0	11.8
	D4	0.1	3.9
Weight	W1	4.8	19.7
	W2	2.4	1.9
	W3	5.8	0.8
	W4	2.8	23.6
Depth	Z1	29.2	0.0
	Z2	3.5	4.0
	Z3	6.0	1.9
	Z4	3.6	1.4
Temperature	T1	28.6	0.0
	T2	1.1	4.3
	T3	4.9	0.6
	T4	6.9	1.8
Explained variance		26.7	13.6
Cumulative		26.7	40.2

in Fig. 5. The factor 1 axis is associated with the temperature–depth relationship which contributes to 84% of the contrast along this axis. Modalities *T*1 and *Z*1 are located at the extreme positive values of this factor 1 axis, the *T*2–*Z*2 modalities are close together, midway between *T*1–*Z*1 and the cloud formed by *T*3–*Z*3 and *T*4–*Z*4. This indicates a strong relationship between temperature and depth. Cold waters are found in shallow depths, waters with intermediate temperatures occur in intermediate depths, and warmest waters are found in deep strata. In contrast, 86% of the second factor is explained by the relative contribution of the catch and distance modalities (Table 3). The four modalities of the catch variable decrease along the second axis whereas the distance variable presents a slight variation (*D*1, *D*2, *D*4, and *D*3). The *D*3 modality (open waters off the ice edge) is the closest to *W*4 (the largest catches).

The coupling of the large sets with the marginal ice zone varies geographically, as can be seen from Fig. 2. This means that the largest catches should occur at the ice edge in the northern part of the Gulf early in January and that as the ice

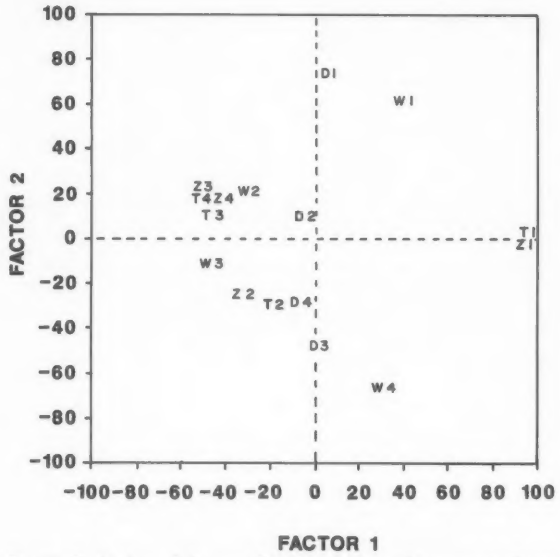

FIG. 5. Projection of the two first factors from the correspondence analysis. See Table 1 for a description of modalities.

cover progresses, these large catches of cod will follow in a southerly direction.

Discussion

Analysis of the data through the use of a log-linear model shows considerable interaction between the four variables, for many of which extensive documentation exists. The most significant of these interactions is between the depth and temperature variable [*ZT*]. The depth component also proved to have a significant effect on code catches [*WZ*] as expected. The significant relationship found between cod catches and the distance to the ice edge [*WD*], however, is observed for the first time.

Temperature is included in the model as an interaction term between depth and distance to the ice edge [*WDZ*] but is not identified as having a significant interaction with cod catches (i.e. [*TW*] term is not significantly different from 0). This three way interaction may be related to variation of cod catches caused by landfast ice. Catches in these shallow areas could be expected to be low because the upwelling in shallow waters causes unsuitable conditions for cod. Buckley et al. (1979) found cold waters (0.0–0.2°C) in the upwelling area at the MIZ in the Chukchi Sea from the surface to a depth of 150 m. Evidence of the importance of the MIZ on observed cod catches is found in the results of the correspondence analysis by the proximity of the *D*3 and *W*4 modalities, but it must be noted that cod catches are not independent from depth and temperature.

From the correspondence analysis, it is not surprising to find that the first axis is associated with a well known physical phenomenon of the presence of cold waters in shallow strata (positive *X* axis) and warmer waters in deep strata (negative *X* axis). Positive values of the *Y* axis are from small catches done in ice cover, while negative values of the *Y* axis are associated with large catches at the ice edge (*D*3). The curvature of the *W*

modalities in the projection of the first two factors illustrates the interaction caused by depth and temperature on cod catches.

Upwelling of deep waters, favorable to the presence of cod, has recently been proven to be a determining factor in the success of the trap fishery in the lower North shore (Rose and Leggett 1988) and on the east coast of Newfoundland (Taggart and Frank 1987). The upwelling is associated with the presence of longshore winds which generate offshore currents to be replaced by bottom waters. The presence of cod in inshore areas is thus limited by a thermal barrier. The same series of events can explain the strong thermal gradients in depths favorable to the presence of cod at the ice edge. The variation in catchability in the MIZ is consistent with the hypothesis of increased fish concentration near the bottom caused by a strong thermal gradient (Jean 1964; Forest and Minet 1981). The thermal gradient is considered to be a more significant cause of variations in catchability than is the presence of prey in the MIZ because cod is found not to be feeding heavily in January.

Observation of increased abundance of cod in the MIZ, coupled with the fact that the ice shows a progression from the estuary to the Cabot Strait would be a significant process in the timing and extent of the winter migration of the 3Pn and 4RS cod stock.

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Characteristics of Coarse Woody Debris for Several Coastal Streams of Southeast Alaska, USA[1]

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Coarse woody debris (>0.2 m in diameter and 1.5 m long) was measured along five undisturbed low-gradient stream reaches; volume, decay class, and horizontal orientation in relation to channel flow of first-, second-, third-, and fourth-order coastal streams were determined. Debris was also classified into four influence zones based on stream hydraulics and fish habitat. Average debris length, diameter, and volume per piece increased with stream size. Eighty percent of debris volume of the first-order and the smaller second-order streams was suspended above or lying outside the bankfull channel, while less than 40% was similarly positioned in the fourth-order stream. Approximately one-third of all debris was oriented perpendicular to stream flow, regardless of stream size. First-, second-, and third-order streams had a higher proportion of recent debris in the channel than the fourth-order stream (≥19 vs. 8%), most new debris being attributable to a major 1984 windstorm. Tree blowdown had a major influence on debris distribution along the smaller stream reaches. Debris jams and accumulations in the largest stream were formed from floated debris. These characterizations are useful for evaluating the distribution and amount of woody debris associated with land-management activities.

Les débris forestiers grossiers (> 0,2 cm de diamètre et 1,5 m de longueur) de cinq tronçons, non touchés par l'homme, de cours d'eau à pente faible ont été mesurés. Leur volume, classe de décomposition et orientation horizontale par rapport au sens d'écoulement de cours d'eau de premier, deuxième, troisième et quatrième ordres ont été déterminés. Les débris ont aussi été classés suivant quatre zones définies par leurs caractéristiques hydrauliques et le type d'habitat qu'elles offrent aux poissons. La longueur, le diamètre et le volume moyens des morceaux augmentaient en raison directe de la taille des cours d'eau. En volume, 80% des débris des cours d'eau de premier ordre et de ceux, plus petits, de deuxième ordre était suspendu au-dessus du chenal de débordement où reposait à côté de ce dernier. Ce pourcentage était inférieur à 40% dans le cas des cours d'eau de quatrième ordre. Environ un tiers de tous les débris était orienté perpendiculairement au courant, quelle que soit la taille des cours d'eau. La proportion de débris récents dans le chenal des cours d'eau de premier, deuxième et troisième ordres était supérieure à celle observée dans les cours d'eau de quatrième ordre (≥19% contre 8%). La plupart des nouveaux débris était dû à un coup de vent violent survenu en 1984. Les arbres déracinés ont eu un effet important sur la distribution des débris le long des plus petits cours d'eau. Les embâcles et les accumulations de morceaux de bois dans les plus gros cours d'eau étaient attribuables aux débris de flottage. Ce genre d'étude s'avère utile pour évaluer la distribution et les quantités de débris forestiers attribuables aux activités d'aménagement du territoire.

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Coarse woody debris (CWD) is an important component of salmonid fish habitat in streams throughout the Pacific Northwest (Bisson et al. 1987). It helps retain organic and inorganic particulate matter that is important for stream stability and biological productivity (Bilby 1984; Speaker et al. 1984). Coarse woody debris also provides structure and hydraulic roughness and can significantly influence habitat for fish and other aquatic organisms (Beschta and Platts 1986). Microhabitats of low-velocity water created by woody debris can be temporary refuges during high stream flow, while during low flow, debris may provide cover and reduce predation (Bustard and Narver 1975; Reiser and Bjornn 1979; Tschaplinski and Hartman 1983).

Coarse woody debris may locally deflect flows, thereby altering stream-bank stability, and floatable debris may damage structures such as culverts or bridges. Debris can also block fish migration (Helmers 1966) and decrease feeding efficiency by blocking out light (Wilzback and Hall 1985). However, its removal to improve fish migration (or for other purposes) has usually been associated with reduced salmonid production (Dolloff 1983; Murphy et al. 1986). Although there is general agreement in recent literature that CWD in streams benefits salmonid production (Harmon et al. 1986), the optimum amount, size, and placement for various streams and fish species have not been specified.

Reiser and Bjornn (1979) and Sullivan et al. (1987) have suggested that the natural or pristine configuration of CWD in

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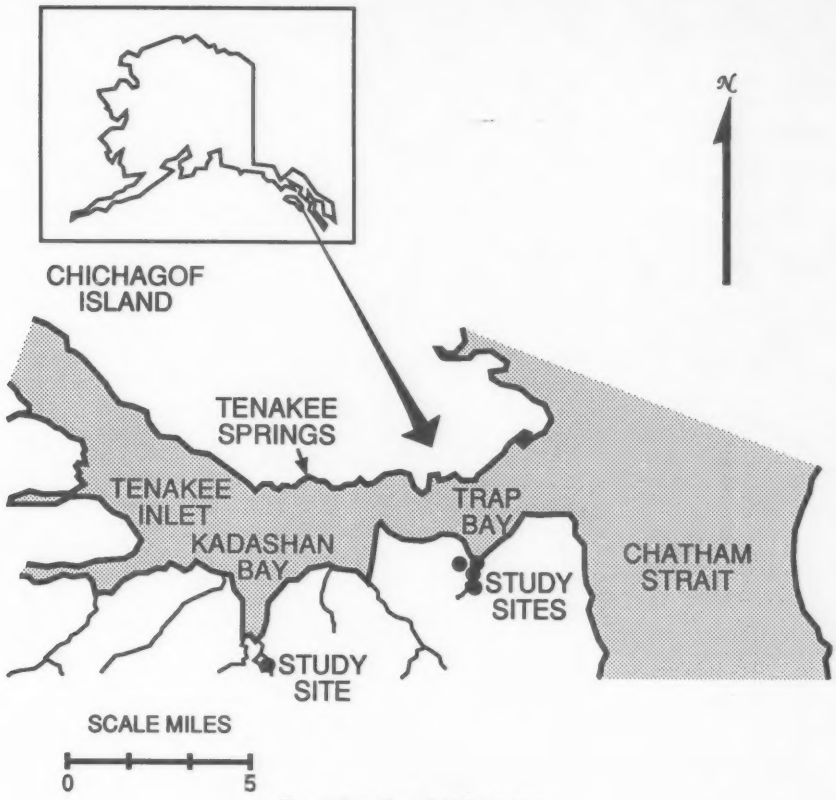

FIG. 1. Location of study streams.

and along streams is desirable because it represents a component of stream habitat to which fish have adapted. Resource managers have often added CWD to streams in an attempt to enhance fish habitat, or have manipulated riparian zones in an attempt to simulate natural conditions, but data on the size and spatial distribution of debris in undisturbed stream systems is largely lacking.

The volume of CWD per unit length or area of stream channel has been used as an index of "stream health" in many studies (Bisson et al. 1987). However, volume measurements seldom differentiate whether CWD is predominantly in a stream, above it, or alongside it. Many studies measure all CWD within a fixed distance from the center of the stream (Andrus et al. 1988). With that technique, a larger proportion of terrestrial CWD will be measured on small streams than on large streams.

This study was undertaken to assess CWD (i.e. pieces greater than 0.2 m in diameter and 1.5 m long) in undisturbed low-gradient stream reaches in southeastern Alaska. We were specifically interested in evaluating the extent to which debris volume, piece characteristics, and spatial distribution varied with stream size.

Study-Site Characteristics

The five streams evaluated in this study are on Chichagof Island in southeast Alaska approximately 115 km southwest of Juneau (Fig. 1); all flow into the Tenakee Inlet. Four of them, Trap Creek, Bambi Creek, Beach Creek, and East Fork Trap Creek, join together and flow into Trap Bay. These streams drain a glacial cirque that is bounded by serrated ridges and a horn peak at the southern end. They have been the subject of previous research on fish populations (Bryant 1984), bedload transport (Campbell and Sidle 1985; Estep and Beschta 1985), riparian vegetation (Sidle 1986), and slope stability (Sidle and Swanston 1982). The fifth and largest stream, the Kadashan River, flows into Kadashan Bay 16 km to the west, draining a much broader glacial valley.

Sitka spruce (*Picea sitchensis*), westen hemlock (*Tsuga heterophylla*), and red alder (*Alnus rubra*) are the overstory tree species (Table 1). Tree basal-area varies from 11–15 m^2/ha along the five streams, alder comprising less than 16% basal area except along the Kadashan River. The number of trees per hectare greater than 0.2 m in diameter at breast height ranges from 55 to 98. A dense understory is dominated by devil's club (*Oplopanax horridum*). Skunk cabbage (*Lysichitum americanum*), blueberry and huckleberry (*Vaccinium* spp.), and salmonberry (*Rubus spectabilis*) are also present.

Coho (*Oncorhynchus kisutch*), pink salmon (*Oncorhynchus gorbuscha*), and Dolly Varden char (*Salvelinus malma*) use the Trap Bay streams (Bryant 1984); those species, plus steelhead trout (*Oncorhynchus mykiss*), and chum salmon *Oncorhynchus keta*) use the Kadashan River drainage.

TABLE 1. Characteristics of the five study streams.

Characteristic	Beach Creek	Upper Bambi Creek	Est Fork Trap Creek	Trap Creek	Kadashan River	Average
Stream order	1	2	2	3	4	—
Watershed[a]						
Area (km^2)	0.72	1.53	5.0	11.4	55.4	—
Elevation (m)						
Minimum	5	5	20	10	15	—
Maximum	615	630	1180	1180	810	—
Stream[a]						
Summer flow[b] (m^3/s)	0.02	0.04	0.30	0.49	1.16	—
2-year peakflow (m^3/s)	1.5	3.0	7.4	13.3	57.8	—
Gradient (%)	1.6	2.3	2.5	1.1	0.8	—
Average low-flow depth (m)	0.24	0.15	0.49	0.58	0.85	—
Average bankfull width (m)	4.9	4.6	8.8	12.8	25.9	—
Study reach						
Length (m)	335	338	457	1530	915	—
Measurement spacing[c] (m)	0.9	0.9	1.5	1.5	3.0	—
Streamside overstory						
Mean number stems/ha	56	77	55	98	62	70
Total basal area (m^2/ha)	15	12	12	15	11	13
Percentage of total basal area						
Red alder	10	16	0	11	25	12
Sitka spruce	59	39	46	55	62	52
Western hemlock	31	45	54	34	13	36

[a]Watershed and stream characteristics were determined for the downstream end of study reaches.
[b]Calculated discharges were based on precipitation and watershed area from Water Resources Atlas for Alaska (USDA Forest Service 1978).
[c]Distance between measurement locations along stream thalweg.

The study reaches on the first-, third-, fourth-, and two second-order streams each had an average gradient of 1.7% (±0.7%) and varied from 335 to 1 530 m in length (Table 1). In all cases they exceeded 35 times the bankfull channel width. Bed material of the reaches consists predominantly of gravel-sized sediment; bedrock or boulder outcrops are uncommon. Average annual precipitation in the area is approximately 165 cm (Sidle and Swanston 1982).

Methods

Along each reach, individual pieces of CWD were characterized by species, volume, location-orientation along the channel, decay class, and grouping. Large-end diameter, average diameter, and length of each piece was measured. Assuming cylindrical shapes, we calculated CWD volumes (m^3) as length × π × (average diameter/2)^2 (Hogan 1987).

We designated four "influence zones" for the stream reaches on the basis of habitat and hydraulic considerations (Fig. 2). Portions of CWD in Zone 1 provide local cover for fish and other aquatic organisms during most of the year, when streams are at low flow. When flows increase during rainfall or snowmelt, CWD in Zones 1 and 2 deflects flows and can cause local scour and fill, affecting the general roughness of a stream. The volume of wood in Zone 3 is a potential source of debris to the channel. Although it does not yet affect a stream hydraulically, it will probably do so in the future. The volume in Zone 4 is another potential source of CWD and, in some cases, its mass and configuration in the terrestrial zone anchor CWD in Zones 1 and 2.

The "influence zones" allow distinction of the volume that could influence fish habitat at low flow (Zone 1), affect stream roughness at high flow (Zones 1 and 2), or eventually enter the channel (Zones 3 and 4). The proportion of a given piece of CWD within each zone was estimated. Debris was measured if any portion was found in Zones 1, 2, or 3; CWD that lay entirely in Zone 4 was not measured (Robison 1988).

The horizontal orientation of each CWD piece was recorded as an angle (0°–180°) relative to the direction of flow (Fig. 3). Precise orientation was often difficult to ascertain because much of the CWD was irregularly shaped, partially decayed, broken, or partially buried in the bank or streambed.

Five decay classes were used to indicate the range from new debris to debris in advanced decay (Table 2). Each debris piece was also characterized as "grouped" (touching another piece) or "ungrouped," and it was noted whether the debris rootwad (if present) was in or out of the channel.

Results and Discussion

Volumes and Characteristics

Total CWD volume per 100 m of stream length increased with stream size while total CWD volume per unit bankfull area (i.e. $m^3/100\ m^2$) decreased (Table 3). Coarse woody debris volumes for Zones 1 and 2, expressed in either unit, increased

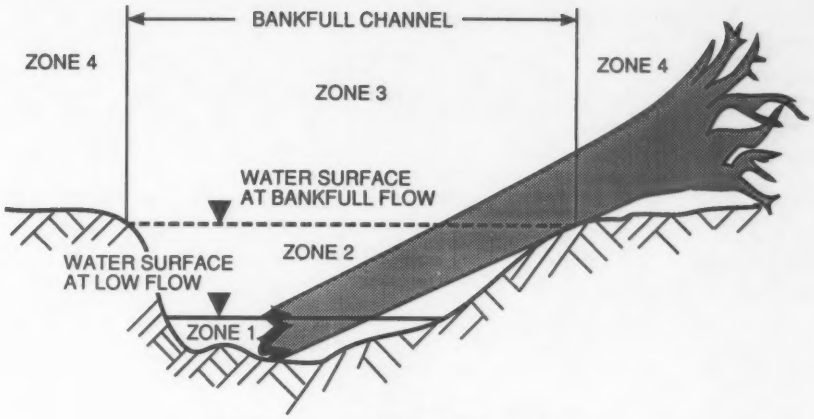

FIG. 2. Coarse woody debris "influence zones."

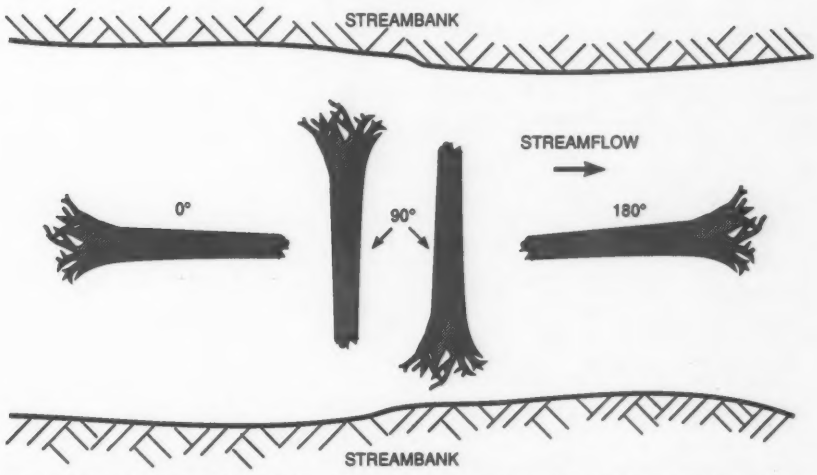

FIG. 3. Method for characterizing horizontal orientation of coarse woody debris in relation to the channel.

with stream size (Fig. 4). Further, the proportion of large CWD pieces within Zones 1 and 2 increased greatly with increasing stream size. For example, the percentage of those pieces with greater than 2 m^3 volume that were lying at least partly in Zones 1 and 2 increased from 10% in the smallest to 56% in the largest stream (Table 3). As stream size increases, larger pieces of CWD are an increasingly important component of the channel environment because they are more stable and less prone to being transported downstream.

The Zone 1 and 2 CWD in this study is similar in definition to the "effective inchannel debris" of Swanson et al. (1984), who found an average loading of 10.1 kg/m^2 for several study streams in southeast Alaska. If a density of 0.5 g/cm^3 is assumed, CWD loadings for Zone 1 and 2 range from 7 kg/m^2 in Beach Creek to 12.5 kg/m^2 in East Fork Trap Creek, which indicates that inchannel debris loadings of streams in both study areas were generally equivalent.

The proportion of CWD within zones changed markedly with stream size (Fig. 5). Approximately 80% of the debris volume in each of the two smallest streams was above or beside the stream (Zones 3 and 4), but in the largest stream, the percentage was less than 40%. There are several reasons for this. In the two smallest streams, average piece length (7.9 and 6.7 m) exceeded average bankfull width (4.9 and 4.6 m); thus, CWD pieces often lay on channel banks with much of their volume suspended above the water surface at bankfull flow. In the two larger and wider streams, trees were more likely to lie partially or entirely in the channel because of greater bankfull widths, which exceeded average piece lengths 1.8 to 3.1 times. As bankfull width increases, even large pieces of CWD can lie completely within Zones 1 and 2.

Approximately 24% of all CWD pieces had volume greater than 2 m^3 (Fig. 6). The number of such pieces ranged from 5.6/100 m of channel on Bambi Creek to 12.3/100 m on the Kadashan River. The average volume per piece for the Kadashan River was 55% greater than that on the other streams (Table 3), and the average length was 8.4 m in comparison to 7.2 m. These results are similar to those for other regions, including those in the northwestern (Bilby 1984) and northeastern United States (Likens and Bilby 1982).

The relatively large piece volumes associated with the Kadashan River may be due to its capacity to transport smaller CWD pieces downstream during high flows. Even with a greater potential for transport, the Kadashan River had 42 pieces/100 m

TABLE 2. A five-class system of evaluating decay of coniferous aquatic coarse woody debris, adapted from Maser and Trappe (1984).

Decay class	Bark	Twigs (3 cm; 1.18 in)	Texture	Shape	Wood color
I	Intact	Present	Intact	Round	Original color
II	Intact	Absent	Intact	Round	Original color
III	Trace	Absent	Smooth; some surface abrasion	Round	Origial color; darkening
IV	Absent	Absent	Abrasion; some holes and openings	Round to oval	Dark
V	Absent	Absent	Vesicular; many holes and openings	Irregular	Dark

TABLE 3. Characteristics of coarse woody debris (CWD) in and along the five study streams. In all instances, % = percentage of pieces, not percentage of volume.

	Stream					
CWD characteristic	Beach Creek	Upper Bambi Creek	East Fork Trap Creek	Trap Creek	Kadashan River	Average
Number pieces measured	83	85	188	514	303	—
Pieces/100 m stream length	25	25	41	34	42	33
Average length (m)	7.9	6.7	6.7	7.3	8.4	7.4
Average large diameter (m)	0.53	0.46	0.51	0.53	0.60	0.53
Volume/piece (m^3)	1.5	1.4	1.5	1.8	2.4	1.7
Volume/100 m stream length (m^3)						
All zones	37	36	60	57	100	58
Zones 1 and 2	7	7	22	24	62	24
Volume/100 m^2 bankfull area (m^3)						
All zones	7.6	7.9	6.7	4.3	3.9	6.1
Zones 1 and 2	1.4	1.6	2.5	1.9	2.4	2.0
Pieces >2 m^3 in zones 1 and 2 (%)	10	10	22	32	56	26
Rootwads in channel (%)	2	6	24	24	20	15
Number rootwads/ 100 m	0.6	1.5	9.8	8.2	8.4	7.1
Grouped (%)	67	58	52	68	72	63
Alder (%)	12	12	4	16	29	15
Decay class (%)						
I and II	30	19	22	24	8	21
III	23	34	27	27	34	29
IV and V	47	47	51	49	58	50

in comparison with only 25 pieces/100 m in the two smallest streams. Frequency of CWD per unit of stream length decreases with an increase in stream size (R. E. Bilby and J. W. Ward, Weyerhaeuser Co., Western Forestry Research Center, Centralia, WA 98531, USA, unpubl. data). The greater frequency of CWD associated with the Kadashan River may be due to relatively high rates of CWD entry. While trees blown over by high wind would fall primarily parallel to the prevailing wind direction, bank cutting may cause them to fall towards a stream. We observed that CWD recruitment due to bank erosion

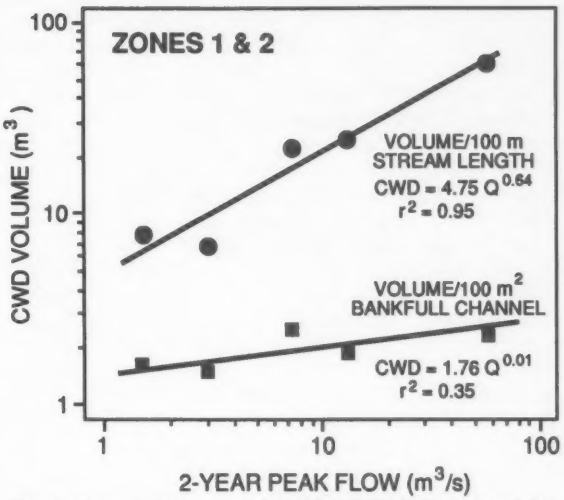

FIG. 4. Volume of coarse woody debris (CWD) in Zones 1 and 2 in relation to 2-yr peak flows of the five study streams.

was more common in the larger streams, which were more likely to meander and shift laterally during periods of high streamflow, thereby recruiting trees or snags. Also, the rootwads of trees falling into a stream because of streambank erosion were often at the channel edge, where larger streams could easily divert around them and incorporate them in the active channel. The relative proportion of rootwads in a channel may thus index the capacity of a stream to move laterally and recruit debris. The proportion of CWD with rootwads in the channel was only 4% for the two smallest streams but 23% for the three largest (Table 3). An average of only one rootwad per 100 m of stream channel was found for the two smallest streams in contrast to 9/100 m for the three largest.

The proportion of grouped CWD pieces ranged from 52 to 72% of the total. There was no trend with stream size (Table 3).

Coarse woody debris in the four smaller streams was of more recent origin than that in the Kadashan River (Table 3). The high percentage of decay classes I and II in the four smaller streams was probably the result of a major windstorm in the fall of 1984 (Roy Sidle, USDA Forest Service, Juneau, AK, pers. comm.), which illustrates the importance of infrequent CWD recruitment. The Kadashan River study reach was either less affected by the windstorm because of topography or less dependent on catastrophic blowdown for CWD recruitment.

The percentage of alder CWD (Table 3) was greatest in the Kadashan River, reflecting the proportion of alder in the riparian forest (Table 1). Field observations and aerial photos show that the greater stream discharge and more active meander bends of this river provide areas for alder to invade, grow, and be recruited during high flow. More alder, other hardwoods, and early successional species may be expected in streams like the Kadashan River because high flows cause local scour and deposition along streambanks and incremental lateral shifting of the channel across the floodplain, periodically resetting vegetation in the riparian area.

Orientation

In contrast to a theoretical frequency distribution of horizontal orientation of debris, which was based on the assumption that riparian trees fall in random direction (Fig. 7A), a high proportion of the actual distribution in relation to stream chan-

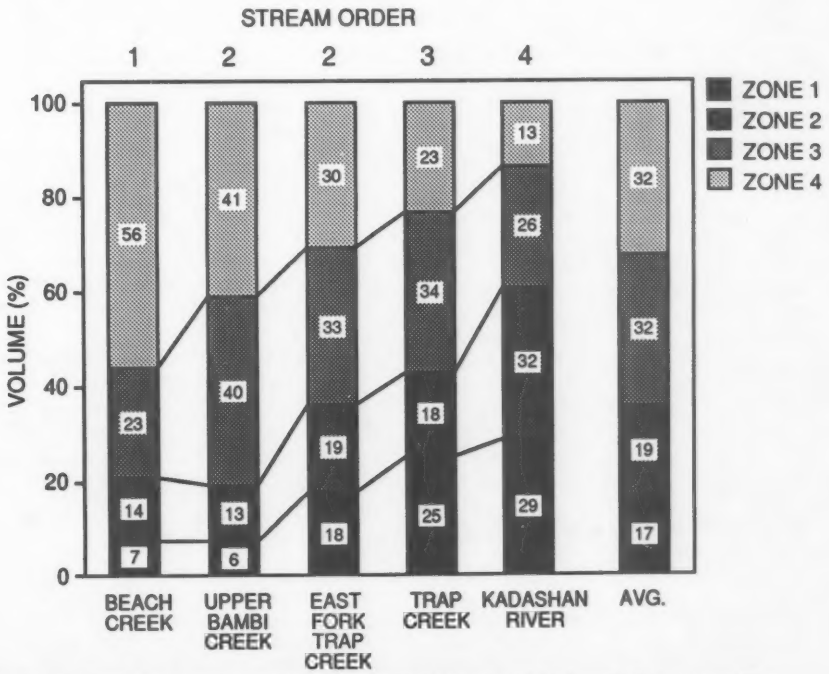

FIG. 5. Percentage of coarse woody debris volume within each of the four "influence zones."

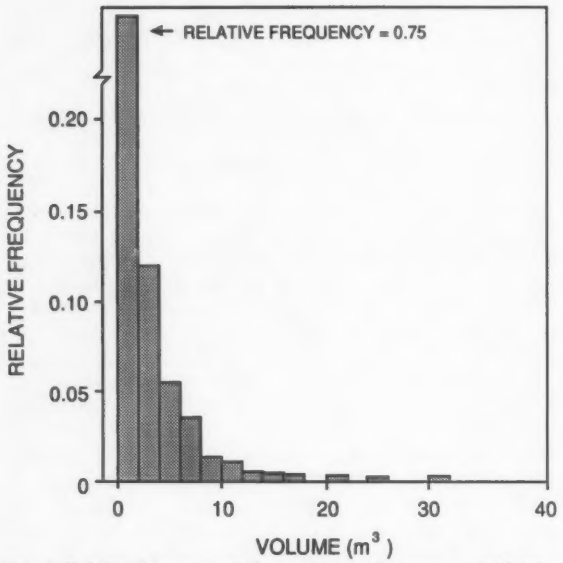

FIG. 6. Relative frequency of piece volumes of coarse woody debris for all study streams.

nels was between 80 and 100° (Fig. 7B, 7C). The peak around 90° may indicate that many trees enter a stream perpendicular to the channel. This orientation may be due to several factors. Streamside branches of riparian trees may receive more light and may have greater biomass than branches away from the stream, creating an unequal weight distribution that could increase the probability of a tree falling towards a stream. Streamside trees (especially alder) may exhibit "phototropism" and lean towards a stream in response to increased light, or bank erosion may cause trees to lean toward a stream. Further, with increasing distance from a channel, the range of horizontal angles at which a tree may fall and still provide large woody debris to a stream becomes more limited, ultimately approaching an angle perpendicular to the channel. The 90° orientation was prevalent regardless of volume, length, diameter, or grouping of CWD.

Hogan (1987) indicates that "stable" or "unmoved" CWD tends to be oriented perpendicular to or "slanted" to the stream channel, while unstable CWD tends to be parallel to the channel. In this study, the frequency of CWD that was relatively parallel to the channel (0°–40° and 140–180°) decreased and the perpendicular orientation (80–100°) increased with piece size (Fig. 7B, 7C), possibly indicating that greater length or volume decreased movement. Bilby (1985) suggests that longer CWD is more stable; it can span the stream width or have sufficient volume outside the active channel to be anchored during high flow. As stream size increased, more CWD was parallel to the channel, and the proportion of pieces with an orientation between 80 and 100° decreased from 34 to 28% (Fig. 7D, 7E, 7F). These shifts seemingly indicate greater potential for CWD transport in larger streams.

Spatial Distribution

The spatial distribution of CWD along the study streams was variable, reflecting the occurrence of episodic blowdown and other factors (Fig. 8). In Bambi Creek, the large peaks between 250 and 300 m along the channel represent local entry from blowdown during a windstorm in 1984. The woody debris at this spot created several side channels and a large sediment-deposition zone.

For medium-sized Trap Creek, CWD volumes indicate nearly continuous debris loading along the stream. However, several relatively large amounts of blowdown on Trap Creek had altered the channel. For example, at channel distance 220 m in Trap Creek (Fig. 8), debris accumulations in the channel caused an island to form.

The Kadashan River had several CWD accumulations (Fig. 8; channel distance 60 and 110 m), but these accumulations did not cause major sediment deposition as in smaller streams. The lack of debris-free stretches interspersed with large debris jams that are characteristic of fourth-order streams (Bisson et al. 1987) was surprising. Apparently, CWD along the Kadashan River is more stable than in streams of comparable size, perhaps because the river is relatively unconfined by hillslopes or high stream banks. At high flow, side channels carry excess water from the main channel so that less is available to transport CWD into jams.

Field observations also indicated little tendency for CWD to occur uniformly along channels. In the smaller streams, debris accumulations tended to be infrequent and largely controlled by the availability of trees susceptible to blowdown. In medium-sized streams, debris accumulations along the channel were more common because channel processes aided recruitment and transport of CWD of smaller size classes. In the largest stream, high-volume debris jams occurred locally, but without regular spatial distribution.

The two smallest streams had some portions with heavy accumulations, while others were almost wood free. Harmon et al. (1986) have suggested that because small streams cannot transport CWD, the entry mechanism dictates spatial distribution. Thus, CWD volumes at a given location are primarily dependent on whether the stream is flowing through an area of blowdown or not.

The occurrence of CWD along the larger second-order and smaller third-order stream in this study was relatively continuous, a finding similar to that of other studies (Bisson et al. 1987). The fourth-order stream also was typified by continuous debris along most of the channel, even though high flows were obviously instrumental in floating and rearranging debris into jams at various points.

In the Oregon Coast Range, Long (1987) found that debris jams or areas of high CWD accumulations occurred immediately downstream from junctions with tributaries of high gradient (>5%). These tributaries came from narrow valleys with steep side slopes, and CWD appeared to enter the main channel as debris torrents. The low-gradient streams evaluated in this study were in wide, alluvial valleys, and debris torrents were not a local source of CWD. There was no discernible relationship between CWD accumulations and tributary junctions.

Conclusions

Our study shows that the amount of CWD and the location with respect to the channel cross-section change with stream size. We therefore recommend that CWD locations be differentiated by stream influence zones in the inventories of forest streams.

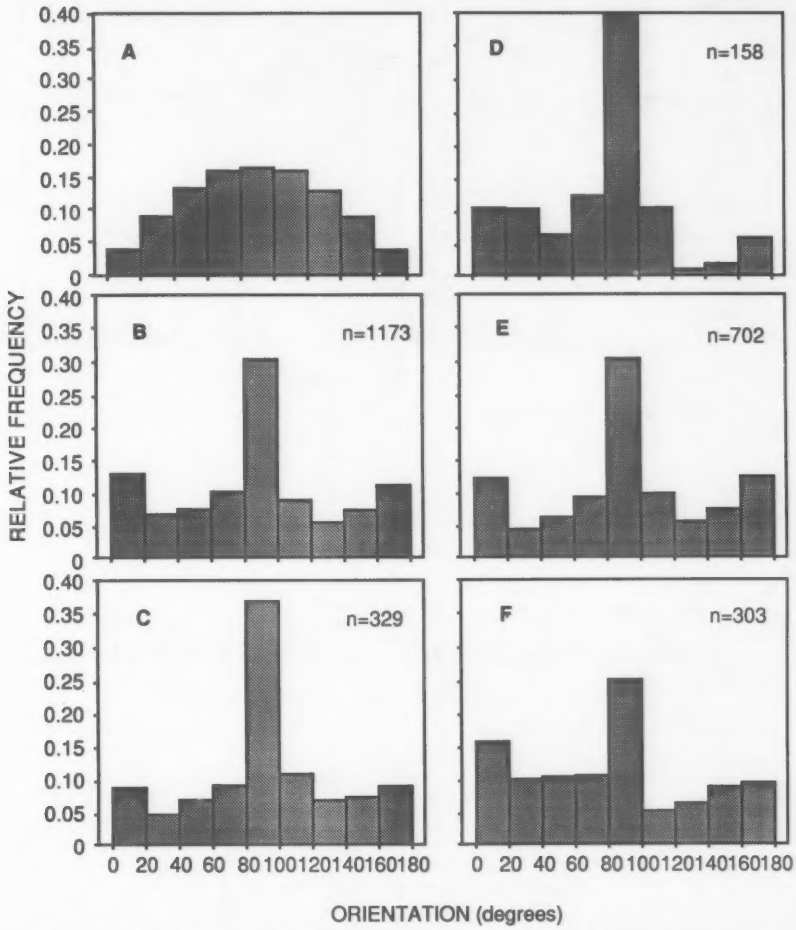

FIG. 7. Relative frequency of horizontal orientations of coarse woody debris (CWD): (A) a theoretical distribution, (B) all CWD in all study streams, (C) pieces >1.8 m^3 in volume in all study streams, (D) Bambi Creek, (E) Trap Creek, and (F) Kadashan River.

The simple computation of average CWD volume per unit of stream length or surface area may not adequately index spatial irregularities in debris accumulations. For instance, one stream may have large CWD jams interspaced with areas of almost no CWD, and another may have evenly spaced CWD. Athough the gross volumes of CWD may be similar, the habitat formed in the two systems may be very different. Large jams can form pools, trap organic matter (Harmon et al. 1986) and cause deposition of sediment immediately upstream, but if such jams are located at only a few places, the overall effect on the stream is localized and limited. Ungrouped CWD does not form pools or store sediments and organic matter as well as jams (Harmon et al. 1986), but because resistance to flow is spread over an entire stream system, it may have a greater overall effect on channel morphology.

The dimensional characteristics of CWD pieces in this study changed with stream size; the average piece volume of CWD was 55% greater on the Kadashan River than in the four smaller streams. The capacity of a large stream to transport woody debris at high flows indicates that larger debris may be needed to provide stability for larger streams. From a forest management perspective, longer rotations would be needed to provide sources of larger CWD.

The perpendicular orientation of much CWD in this study probably indicates that it is stable (Hogan 1987). R. E. Bilby and J. W. Ward (Weyerhaeuser Co., Western Forestry Research Center, Centralia, WA, 98531, USA unpubl. data) found that such CWD tends to span the channel and provide "plunge" rather than backwater pools. It appears that orientation has important effects on the types of pools formed, and thus on fisheries habitat.

We found no systematic spacing of CWD along these undisturbed streams in southeast Alaska. The irregular spacing of individual debris pieces and accumulations may provide maximum variability of debris-influenced habitat.

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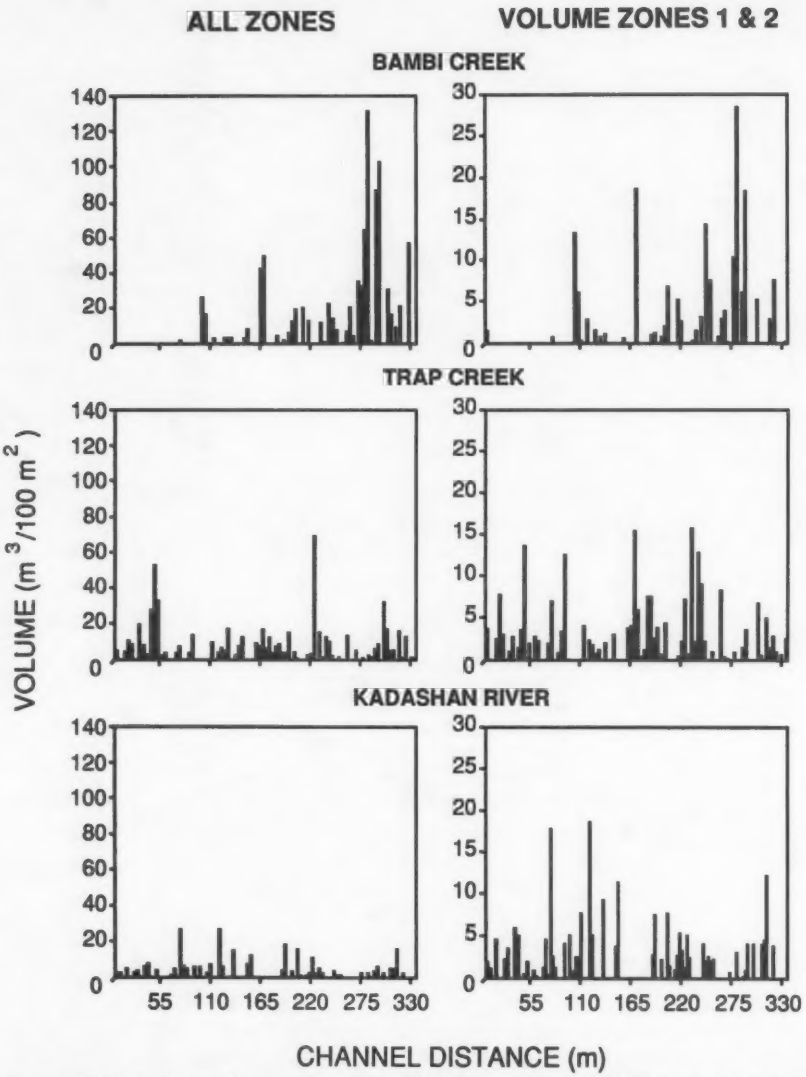

FIG. 8. Spatial distribution of the volume per bankfull surface area for selected 330-m reaches of three study streams (the width of each bar represents 3 m of stream length).

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Effects of Calcium and pH on the Reproductive Success of *Amnicola limosa* (Gastropoda)

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Shaw, M. A., and G. L. Mackie. 1990. Effects of calcium and pH on the reproductive success of *Amnicola limosa* (Gastropoda). Can. J. Fish. Aquat. Sci. 47: 1694–1699.

Field and laboratory experiments were designed to examine the relationship between water chemistry (especially pH and calcium) and the reproductive success of *Amnicola limosa*. Fecundity (no. eggs·female^{-1}) was positively correlated with lake buffering capacity ($P=0.002$) in naturally occurring populations. We documented a 66% reduction in fecundity in lakes over a pH range of 7.6–5.8. However, fecundity was higher than expected in a highly-coloured, low-pH lake. The number of juveniles produced per egg was not related to any water chemistry variable (multiple $R^2=0.186$). A laboratory experiment demonstrated that pH, and not calcium, was limiting embryonic development. All embryos held at pH 4.5 failed to hatch. Eggs held at pH 5.5 experienced reduced hatching success ($P=0.013$) and delayed development ($P<0.001$) compared with those held at pH 6.5. Length of newly hatched snails did not differ significantly between treatments ($P=0.891$). The critical calcium concentration required for embryonic development in laboratory incubation lay between 0.14 and 1.11 mg·L^{-1}. This is well below the calcium concentration of acidifying lakes in south-central Ontario.

Des expériences sur le terrain et en laboratoire visant à examiner la relation entre les propriétés chimiques de l'eau (particulièrement le pH et la teneur en calcium) et le succès de reproduction d'*Amnicola limosa* ont été effectués. La fécondité (nombre d'oeufs·femelles^{-1}) était positivement corrélée avec le pouvoir tampon des lacs ($P=0,002$) dans des populations vivant en nature. Quand le pH des lacs passe de 7,6 à 5,8, la fécondité diminue de 66%. Cependant, la fécondité était supérieure à ce qui était attendu dans un lac dont le pH était bas et l'eau, très colorée. Le nombre de juvéniles produit par oeuf n'était corrélé avec aucun des paramètres de l'eau (R^2 multiple$=0,186$). En laboratoire, il a été démontré que le développement embryonnaire était limité par le pH, et non par la teneur en calcium. Aucun des embryons exposés à un pH de 4,5 n'a éclos. Les oeufs exposés à un pH de 5,5 ont connu un succès d'éclosion réduit ($P=0,013$) et un développement tardif ($P<0,001$) comparé à ceux exposés à un pH de 6,5. La longueur des gastéropodes au moment de l'éclosion ne différait pas de façon significative selon les traitements ($P=0,891$). La concentration critique de calcium nécessaire pour permettre le développement des embryons en laboratoire se situait entre 0,14 et 1,11 mg·L^{-1}. Cette concentration est de beaucoup inférieure à la concentration de calcium dans les lacs acides du centre sud de l'Ontario.

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Evidence from laboratory and field studies indicate that gastropods are very sensitive to acidification. Field surveys show that reductions in species number and relative abundance accompany trends in pH decline (Aho 1966; Roff and Kwiatkowski 1977; Okland 1980; Dillon and Benfield 1982; Servos 1983). In situ experiments reveal that productivity (Rooke and Mackie 1984), and growth and survival (Rooke and Mackie 1984; Servos et al. 1985; Shaw and Mackie 1989) decline below pH 6.0. Losses of mollusc populations linked to acidification have occurred in Sweden (Mossberg 1979) and Canada (Rooke and Mackie 1984; Shaw and Mackie 1989). Laboratory experiments confirm that snails, especially the embryonic stages, are sensitive to H^+ ions (Garve 1980; Holcombe et al. 1984; Servos et al. 1985).

The mechanisms leading to population decline are fairly well understood for at least one snail species: *Amnicola limosa*. Reduced growth and productivity of *A. limosa* at pH's below 6.0 have been observed in lakes in south-central Ontario (Rooke and Mackie 1984; Servos et al. 1985). Shaw and Mackie (1989) found that recruitment failure due to reductions in fecundity and hatchling survival could account for the year-class failure (1983) and subsequent elimination of this species from Heney Lake (pH 5.70).

Although we understand why this species has declined in some low-pH lakes, the stresses contributing to its reproductive failure and elimination are less well known. Multivariate analyses of field survey data have shown that water hardness and pH are good predictors of species number and/or abundance in Norway (Okland 1983), Finland (Aho 1966), and Canada (Mackie 1987). However, Okland (1983) noted that nine of 11 common snail species had increased tolerance to low pH with increasing calcium concentrations. Calcium is known to be physiologically important for snail growth and development. Laboratory experiments have shown that the growth of several snail species is inhibited at low calcium concentrations (Thomas et al. 1974; Nuduku and Harrison 1980). Calcium carbonate accounts for 80–95% of freshwater molluscan dry weight (Mackie and Flippance 1983). However, indications that low

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calcium concentrations, typically found in lakes sensitive to acidification, might contribute to reproductive impairment have not been investigated.

The purpose of this study was to examine the relationship between water chemistry (especially pH, and calcium) and the reproductive success of *A. limosa*. We first performed an in situ field experiment to document the reproductive success of naturally occurring *A. limosa* populations over a range of pH, alkalinity, and Ca^{2+} levels, and to elucidate which water chemistry variables best explained the observed variability in fecundity and juvenile success. Since water hardness variables were confounded in the field data set, a laboratory factorial experiment was necessary to separate the effects of pH and Ca^{2+} on embryonic development. The field and laboratory studies were designed to test whether low pH or Ca^{2+} levels typical of acidifying lakes contributed to the reproductive impairment of *A. limosa*. An evaluation of the factors contributing to the failure of acid sensitive organisms will help strengthen the link between lake acidification and population losses.

Study Area

Thirty lakes near Dorset, Ont., representing a wide range of pH, alkalinity, and Ca^{2+} concentrations were surveyed for *A. limosa*. From these lakes, 23 with viable *A. limosa* populations were chosen for study (Fig. 1). Mean summer epilimnetic pH and alkalinities ranged from 5.8 to 7.7 and 0.9 to 15.1 mg $CaCO_3 \cdot L^{-1}$ respectively. Calcium ion concentrations ranged from 2.2 to 6.5 $mg \cdot L^{-1}$. Water chemistry and lake location data for 19 of these lakes from which experimental data were collected is available upon request.

Methods

Lake Survey Experiment

Fecundity and juvenile success (no. juveniles·egg^{-1}) were measured in 23 lakes to determine if the reproductive success of *A. limosa* varied in lakes over a range of chemical conditions. Twenty-five reproductively mature individuals were collected and incubated throughout the reproductive period (late May to late August) in each lake. Snails were introduced in five groups of five into 500-ml polyethylene cages with the tops and bottoms replaced with 480-μ nylon mesh. Cages were attached in groups of five to an acrylic strip with nylon nuts and bolts. The cages were weighted with rocks in approximately 0.5 m of water near the outflow of each lake. Goldstein et al. (1984) suggested that outflow conditions best represent an integration of lake water chemistry as a whole.

Conditioned leaf litter was used to provide a source of food for the snails and was replenished (if necessary) at monthly intervals. Animals were placed in the cages on May 19–24, 1985. Lakes were revisited on June 24–29, 1985 when the sex of adults was determined. Dead adults were removed from cages on subsequent visits. The number of eggs laid in each container was recorded after 36 (June 24–29) and 90 d (August 23–September 3) of incubation. The numbers of eggs and juveniles in each cage were recorded from 18 and 14 lakes, respectively. The cages from the remaining lakes were lost.

Fecundities were expressed as the no. eggs·$female^{-1}$·$cage^{-1}$ and juvenile success was expressed as the no. juveniles·no. $eggs^{-1}$·$cage^{-1}$. Lake average fecundity and juvenile success values were determined by averaging results from the

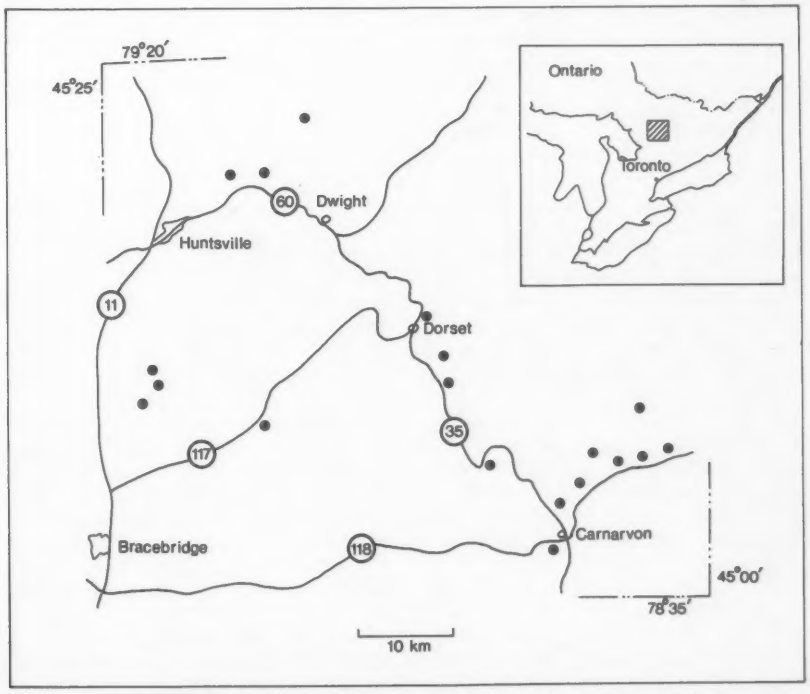

FIG. 1. Location of 19 lakes in south-central Ontario where the reproductive success of *A. limosa* were examined.

TABLE 1. Nominal and measured pH values (with standard errors) for all treatments in the laboratory pH/calcium bioassay. *N* represents the number of measurements.

Nominal pH	Measured pH (SE)	Replicate	*N*
4.5	4.53 (0.02)	1	46
	4.56 (0.02)	2	66
	4.54 (0.02)	3	77
	4.57 (0.03)	4	72
5.5	5.53 (0.02)	1	64
	5.55 (0.02)	2	31
	5.52 (0.02)	3	97
	5.53 (0.02)	4	78
6.5	6.43 (0.03)	1	93
	6.42 (0.04)	2	83
	6.43 (0.03)	3	97
	6.45 (0.03)	4	84

five cages per lake. Principal components analysis (PCA) was used to derive orthogonal (i.e. independent) components from selected water chemistry variables. All data (with the exception of pH) were tested for normality and subsequently logged. Quartimax rotation was applied to isolate the effects of each variable on a single component. Separate multiple linear regressions were performed using the PC scores as independent variables and fecundity and juvenile success as dependant variables. All statistical analyses were performed using SYSTAT 4.0 (Wilkinson 1988).

Laboratory Calcium/pH Bioassay

Because water buffering capacity variables were positively correlated in the survey lakes, a laboratory bioassay was necessary to separate the effects of calcium and pH on the embryonic development of *A. limosa*. The range of pH and Ca^{2+} levels was chosen to represent those typically encountered in soft water shield lakes. A 3 × 3 factorial design was chosen with nominal pH levels of 4.5, 5.5, and 6.5, and nominal Ca^{2+} concentrations of 0, 1.5, and 4.5 mg·L^{-1}. We employed a static bioassay with complete water renewal every 48 h. Each of the nine treatments was replicated four times, and all treatment units were incubated at 21°C on a 16 h light, 8 h dark cycle.

We simulated soft water typical of Canadian Shield lakes by adding 1 mL of an acidified electrolyte stock solution per litre of double-deionized water. The test solution was then acidified to pH 4.0 with 0.1N H_2SO_4, and $CaCl_2$ was added to three batches of test water to achieve nominal calcium levels of 0, 1.5, and 4.5 mg·L^{-1}. We adjusted subsamples to the desired pH levels (4.5, 5.5, 6.5) with 0.1N KOH. Finally, 0.1N K_2SO_4 was added to the pH 4.5 and 5.5 treatments to maintain equivalent levels of K^+ in all treatments. In this way, the total ionic concentrations in the nine treatments were kept similar. Water was stirred for a minimum of 5 min to ensure adequate mixing, allowed to stand overnight, and adjusted for pH (if necessary) the following day before *A. limosa* eggs were introduced. Treatment pH's were measured and adjusted daily thereafter (Table 1). Triplicate water samples of the nine treatments were submitted to the Ontario Ministry of the Environment for major ion analysis (Table 2). Measured Ca^{2+} concentrations were 0.14, 1.11, and 3.41 mg·L^{-1} at nominal levels of 0, 1.5, and 4.5 mg·L^{-1}, respectively.

We obtained *A. limosa* eggs from several hundred adults collected from Green Lake (pH 7.6). Glass growth dishes with 10 adults held in Green Lake water and sediment were examined daily for the presence of eggs. A total of ten eggs at the same developmental stage were randomly assigned to each of the 36 100-mL polyethylene test containers. The volume of test water exceeded the level of 2 L per gram of test organism per day recommended by ASTM (1980). For the first 8–9 d, eggs were examined under the microscope daily for viability and stage of development. Thereafter, they were inspected every 2 d. Egg development was categorized into one of 8 easily recognized stages (single cell, 2–8 cells, multicellular, gastrula, trochophore, early shelled, late shelled, and hatched) as classified by Wada (1968). We documented the number of days to hatch, percent hatching success, length of hatchlings and survival time (for those treatments in which eggs failed to hatch). Tests were terminated when all the embryos had either died or hatched.

The median number of days to hatch, or days to death (for treatments in which hatching did not occur) were estimated by log-probit plots. Hatching success, days to hatch, and length at hatch were analyzed separately using two-way unbalanced Analysis of Variance (ANOVA) designs. A one-way ANOVA was computed for the time to death data for all treatments at pH 4.5, and for all treatments with 0 calcium levels.

Results from two of the 36 replicate treatment containers were not included in the analysis (pH 5.5, 1.5 mg Ca·L^{-1}, rep. 2; and pH 5.5, 4.5 mg Ca·L^{-1}, rep. 1). In both cases, all 10

TABLE 2. Major ion concentrations for treatments in the laboratory pH/calcium bioassay. All concentrations are in mg·L^{-1}.

Ion	Concentration (SE)	*N*	Treatment
Calcium	0.14 (0.11)	3	0.0 mg·L^{-1} Ca
	1.11 (0.04)	3	1.5 mg·L^{-1} Ca
	3.41 (0.07)	3	4.5 mg·L^{-1} Ca
Chloride	0.50 —	1	0.0 mg·L^{-1} Ca
	2.50 —	1	1.5 mg·L^{-1} Ca
	6.50 —	1	4.5 mg·L^{-1} Ca
Magnesium	0.78 (0.01)	9	all treatments
Sodium	0.83 (0.12)	9	all treatments
Potassium	2.64 (0.07)	9	all treatment
Sulphate	8.15 (0.21)	9	all treatment

TABLE 3. Loadings of water chemistry variables onto five rotated principle components for 23 lakes. Values ≥0.75 are underlined.

Variable	PC1 (buffering capacity)	PC2 (DOC)	PC3 (nutrients)	PC4 (Na)	PC5 (colour)
Alkalinity	0.983	−0.054	0.046	0.077	0.044
Calcium	0.972	0.105	−0.049	0.021	0.078
pH	0.967	−0.082	0.023	0.119	0.028
DOC	−0.029	0.980	0.064	−0.048	−0.177
Total Phosphorus	0.003	0.075	0.979	−0.159	−0.099
Sodium	0.417	−0.087	−0.251	0.860	0.128
Colour	−0.338	0.417	0.186	−0.156	−0.808
Cumulative (%) variance explained	44.8	61.5	76.7	88.3	98.5

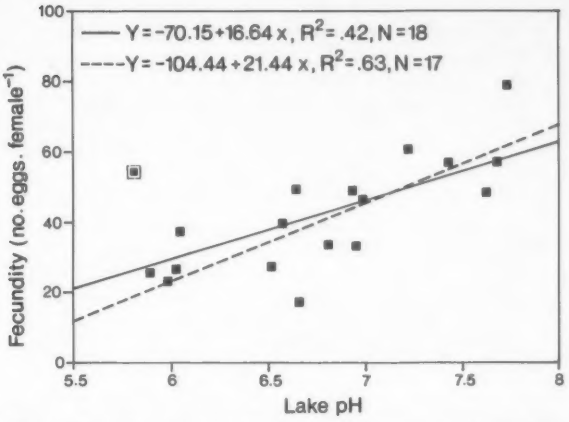

FIG. 2. Fecundity (no. eggs·female^{-1}) of *A. limosa* vs. lake pH. The solid line represents the regression for 18 lakes. The dotted line represents the regression excluding Fawn lake ($N = 17$).

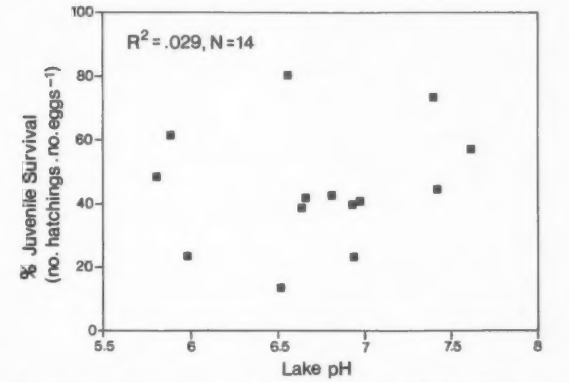

FIG. 3. Juvenile success (no. juveniles·no. eggs $^{-1}$) of *A. limosa* vs. lake pH.

apparently healthy embryos died overnight. This mortality was atypical of the other replicate treatments (including pH 4.5). Therefore, we surmised the sudden mortality was due to causes other than the experimental conditions, and excluded these data from the analysis.

Results

Lake Survey Experiment

Principal Component Analysis (PCA) of the selected water chemistry variables produced five interpretable components: buffering capacity, DOC, total phosphorus, sodium, and colour respectively (Table 3). These five components retained 98.6% of the total variance of the original data set. Although 65% of the variance in fecundity could be explained by the five components in a multiple linear regression, buffering capacity (factor 1) was the only significant variable ($P = 0.002$). Lake pH alone explained 42% of the variation in fecundity in a simple linear regression ($P = 0.003$, $R^2 = 0.42$). A plot of fecundity vs. pH revealed that snails from the lowest pH lake (Fawn, pH = 5.89) exhibited unusually high fecundities (Fig. 2). Fawn Lake was also the most highly coloured lake in the data set

TABLE 4. Summary of *A. limosa* embryonic responses to the range of pH and calcium levels in the laboratory experiment. Time to hatch and survival time expressed as median no. days. Values in a column followed by the same symbol are not significantly different ($P = 0.05$).

	Treatment				
pH	Calcium (mg·L^{-1})	Hatching success (%)	Time to hatch (d)	Length at hatch (mm)	Survival time (d)
	0.14	0.0	—	—	3.8*
4.5	1.11	0.0	—	—	4.3*
	3.41	0.0	—	—	11.9*
	0.14	0.0	—	—	9.5+
5.5	1.11	66.7*	26.7*	0.81*	—
	3.41	43.3*	27.0*	0.87*	—
	0.14	0.0	—	—	20.5*
6.5	1.11	91.4*	22.3+	0.84*	—
	3.41	100.0+	21.6+	0.85*	—

(109 cobalt units). When this point was removed from the data set, the R^2 value increased to 0.63 (comparable to the R^2 from the multiple linear regression). Thus, lake pH explained 63% of the variation in fecundity in clear lakes.

The relationship between lake water chemistry factors and juvenile success was not significant ($P = 0.858$, multiple $R^2 = 0.186$). pH was not a good predictor of juvenile success in lakes (Fig. 3) presently supporting viable populations of *A. limosa*.

Laboratory Calcium/pH Bioassay

There was an apparent linear trend between pH and hatching success of *A. limosa*. No embryos hatched at pH 4.5, while percent hatch was significantly lower at pH 5.5 (55%) than at pH 6.5 (95.7%) ($P = 0.013$) (Table 4). The effect of pH on median days to hatch was significant at $P < 0.001$. Embryos incubated at pH 5.5 took on average 25% longer to hatch than those at pH 6.5. Increasing the pH in the lowest Ca^{2+} treatments (0.14 mg·L^{-1}), where no hatching occurred, resulted in significantly longer median survival times ($P < 0.001$). Embryos held at pH 4.5, 5.5, and 6.5 at Ca^{2+} levels of 0.14 mg·L^{-1}, died on average after 3.8, 6.5, and 9.5 d, respectively (Table 4).

The overall effect of Ca^{2+} on embryonic development was also apparent. All embryos held at 0.14 mg·L^{-1} Ca^{2+} failed to hatch regardless of pH. However, increasing the Ca^{2+} concentration from 1.11 to 3.41 mg·L^{-1} had no effect on hatching success ($P = 0.596$) or time to hatch ($P = 0.923$) (Table 4). Although there was an apparent trend towards greater median survival times at pH 4.5 with increasing Ca^{2+} levels, this effect was not significant ($P = 0.195$).

There was no significant difference in the average length of newly hatched snails incubated at different pH ($P = 0.891$) and Ca^{2+} concentrations ($P = 0.351$) (Table 4).

Discussion

A survey of reproductive success of *A. limosa* in 18 soft-water Canadian Shield lakes revealed a strong relationship between water buffering capacity and fecundity for naturally occurring populations. Based on the line fitted for the lake pH/fecundity relationship (excluding Fawn Lake), females at pH 7.6 produced on average 58.5 eggs·season^{-1}, compared to

19.9 eggs·season^{-1} at pH 5.5. This represents a 66% reduction in reproductive output over the range of lakes studied. Shaw and Mackie (1989) also documented a significant positive relationship between lake pH and fecundity in a field transplant experiment with this species.

Decreased fecundity may be due in part to the smaller size of this gastropod in low pH/alkalinity evironments. Servos et al. (1985) and Rooke and Mackie (1984) demonstrated that *A. limosa* grew more slowly in lakes with low buffering capacities. Laboratory experiments confirm that gastropod growth is inhibited at low pH (Thomas et al. 1974; Garve 1980), and at low calcium levels (Thomas et al. 1974; Nuduku and Harrison 1980); (in the study by Thomas et al., however, increases in calcium concentrations were accompanied by increasing pH). Shaw (1987) documented a positive length–fecundity relationship for this species under field conditions. These data indicate that reduced fecundity in poorly buffered lakes is a direct consequence of smaller adult size.

The relationship between buffering capacity and fecundity did not hold true for a highly coloured, low-pH lake (pH = 5.81). Fawn Lake adults exhibited greater average lengths and higher fecundities (54.3 eggs·female^{-1}) than did snails in clear, similar-pH lakes. Shaw and Mackie (1989) found that snails from another coloured lake (Dickie Lake, pH 5.89) also exhibited higher than expected fecundities. High molecular weight organic acids present in coloured lakes are known to reduce the bioavailability and toxicity of trace-metals to aquatic organisms (Winner 1985; Hutchinson and Sprague 1987). The complexation of metals in highly coloured lakes could presumably reduce sublethal metal stress (if any) on *A. limosa*. An investigation into the possible roles DOC and metals play in the reproductive success of *A. limosa* would be helpful in interpreting the field results.

There was no evidence that lake buffering capacity affected juvenile success in naturally occurring populations of *A. limosa*. Shaw and Mackie (1989) showed that hatching success was uniformly high (88–97%) in lakes at pH 5.59–7.42. However, when juveniles were transplanted into lakes where populations had recently disappeared (pH 5.59, 5.70), survival was significantly impaired. They concluded that reduced fecundity and juvenile survival could account for the recent disappearance of this species from Heney Lake (pH 5.59) and possibly from Plastic Lake (pH 5.70). Results from the present study confirm the relationship between fecundity and lake buffering capacity (Shaw and Mackie 1989), but we failed to document any decrease in juvenile success in viable populations of *A. limosa* (i.e. above pH 5.80). These data show that while fecundity decreases linearly with pH, juvenile success is critically impaired only when pH drops below 5.80.

Shaw and Mackie (1989) found no evidence that failure to hatch contributed to the decline of field populations of *A. limosa* at pH 5.59–5.70, but that eggs incubated at pH 4.62 died at a very early developmental stage. This study demonstrated significant decreases in laboratory hatching success of pH 5.5 and a decline to 0% hatch at pH 4.5. Servos et al. (1985) found that while hatching did not occur at pH 5.0, percent hatch was not impaired at pH 5.5 (compared to controls at pH 5.0–6.5). Differences between Servos' findings and those of the present study could be due to the test water used in the two experiments. Servos et al. (1985) acidified lake water to the desired pH with H_2SO_4, while our test water was constituted in the laboratory. Despite these conflicting results, the field and laboratory data indicate that a pH of ≥5.5 is critical for successful hatch in *A. limosa*.

Delayed hatch has been documented in the laboratory at pH 5.5 (this study; Servos et al. 1985). Shaw and Mackie (1989) noted a correlation between delayed embryonic development and decreased juvenile survival in the field. Further research on the survival of hatchlings under different pH and calcium levels in the laboratory is needed to confirm field observations that embryos which take longer to hatch also exhibit higher juvenile mortality.

Amnicola limosa does not require high Ca^{2+} concentrations for embryonic development. All embryos incubated at 0.14 mg·L^{-1} Ca^{2+} in the laboratory failed to hatch, and 82% failed to form a shell in the later stages of development. Only 5% of embryos at ≥1.11 mg·L^{-1} Ca^{2+} levels failed to form shells. There were no significant differences in days to hatch, hatching success, or survival times for those organisms raised at 1.11 and 3.41 mg·L^{-1} Ca^{2+}. Clearly, the critical calcium level required for embryonic development and hatching lies between 0.14 and 1.11 mg·L^{-1}. This level is well below that of the soft-water lakes exhibiting reduced reproductive success. Thus pH (or pH-related factors) appears to be the important factor in affecting the reproductive success of *A. limosa* in clear soft-water Canadian Shield lakes in south-central Ontario.

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Soluble Fluorescence: Effects on Chlorophyll Determination at Different Salinities

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Measurements of 3-(3,4-dichlorophenyl)-1,1-dimethylurea (DCMU) enhanced fluorescence (F_{DCMU}), provided reliable estimates of phytoplankton biomass along a salinity gradient when adjusted for soluble enhanced fluorescence (S_{DCMU}, <1 μm size fraction). Positive linear relationships ($P<0.0001$) were observed between F_{DCMU} and extracted chlorophyll at salinities of ~0, 5, 10 and 30 in experimental mesocosms and the Pawcatuck River Estuary, Rhode Island, both before and after subtraction of S_{DCMU}. Adjusting for S_{DCMU} did not reduce variability in the F_{DCMU} to extracted chlorophyll relationships or alter slopes of the regression equations at different salinities. Positive intercepts (which varied with salinity) were, however, reduced to zero after correction. Results further indicated that S_{DCMU} decreased with increasing salinity (primarily as a result of dilution with seawater), that it was relatively constant at a given salinity, and was unrelated to total F_{DCMU}. Relying solely on in vivo fluorescence techniques, without correction for soluble fluorescence, would thus increasingly lead to overestimates of phytoplankton biomass at decreasing salinities. Over the experimental period, 32% (range 8–93%) of total F_{DCMU} was present in the soluble fraction (S_{DCMU}), with the majority (83%) non-photosynthetic material and most likely dissolved humic substances. S_{DCMU} and light extinction coefficients were significantly and positively related in the mesocosms and the field.

Des dosages du produit à fluorescence accrue (F_{DCMU}) par le 3-(3,4-dichlorophényl)-1,1-diméthylurée (DCMU) ont fourni des évaluations fiables de la biomasse du phytoplancton le long d'un gradient de salinité corrigé pour tenir compte du produit soluble à fluorescence accrue (S_{DCMU}, fraction de taille <1 μm). Un rapport linéaire positif ($P<0,0001$) a été observé entre F_{DCMU} et la quantité de chlorophylle extraite pour des salinités d'environ 0, 5, 10 et 30 dans des mésocosmes, avant et après avoir soustrait la quantité de S_{DCMU}. Le fait de corriger pour la quantité de S_{DCMU} n'a pas réduit la variabilité de F_{DCMU} par rapport à la quantité de chlorophylle extraite ou modifier les pentes des équations de régression pour différentes salinités. Des coordonnées à l'origine positives (qui variaient avec la salinité) étaient, toutefois, réduites à zéro après correction. Les résultats ont montré de plus que la quantité de S_{DCMU} diminuait lorsque la salinité augmentait (surtout à la suite de la dilution avec de l'eau de mer), que la quantité était relativement constante pour une salinité donnée, et qu'elle n'était pas liée à la quantité totale de F_{DCMU}. Le fait de se fonder uniquement sur des techniques de fluorescence in vivo, sans correction pour tenir compte des produits solubles fluorescents, conduirait donc de plus en plus à des surestimations de la biomasse du phytoplancton lorsque la salinité diminue. Au cours de la période expérimentale, 32% (plage de 8 à 93%) de la quantité totale de F_{DCMU} était présente dans la fraction soluble (S_{DCMU}), la majorité (83%) étant du matériel non photosynthétique et plus vraisemblablement des substances humiques dissoutes. Il existait une relation significative et positive entre les coefficients d'extinction du S_{DCMU} et de la lumière dans les mésocosmes et sur le terrain.

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The search for a rapid and reliable method of estimating phytoplankton biomass has led increasingly to the use of in vivo fluorescence techniques, with (F_{DCMU}) or without (IVF) the addition of DCMU — [3-(3,4-dichlorophenyl)-1,1-dimethylurea], a photosynthetic inhibitor (Slovacek and Hannon 1977; Owens et al. 1980; Bates and Platt 1984; Keller 1987). Falkowski and Kiefer (1985) in their review of the theoretical and applied aspects of fluorescence methods noted the success of numerous studies in measuring in vivo chlorophyll concentrations from the fluorescent intensity of water. However, they further acknowledged that the fluorescence intensity to extracted chorophyll *a* relationship could be quite variable. Sources of variation have generally been attributed to species composition (Yentsch and Yentsch 1979; Vincent 1983), size class (Alpine and Cloern 1985), light intensity (Kiefer 1973; Neori et al. 1984), nutrient stress (Kiefer 1973) and diel periodicities (Prézelin and Ley 1980).

In addition to the above, soluble fluorescence (i.e., the fluorescence remaining in a water sample after filtration) may also account for a significant portion of the variation in IVF per unit extracted chlorophyll *a* (Vincent 1981; Carlson and Shapiro 1981). Particularly in freshwater and to varying degrees in estuaries and the open sea, some portion of the fluorescence usually ascribed to chlorophyll *a* is from soluble substances and may lead to anomolously high values of in vivo chlorophyll *a*.

On occasion, fluorescence measurements have been adjusted by subtracting soluble fluorescence from IVF or F_{DCMU} before comparison with standing crop as chlorophyll *a* (Carlson and Shapiro 1981; Alpine and Cloern 1985; Keller 1987). Carlson and Shapiro (1981) described a significant improvement in the fluorescence to chlorophyll *a* relationship in freshwater after such an adjustment was made. Although Alpine and Cloern (1985) similarly corrected total IVF measurements for samples

from San Francisco Bay, they did not discuss the effects of this correction on subsequently developed relationships between *in vivo* and extracted chlorophyll *a*. Keller (1987) found no improvement in the correlation between DCMU-enhanced fluorescence and primary production after adjusting for soluble fluorescence but noted that further investigation was needed.

Concentrations of soluble fluorescence have been qualitatively linked to salinity, with lower values associated with high salinity in estuaries (Tunzi et al. 1974; Loftus and Seliger 1975). In the open sea, soluble fluorescence was thought to originate solely from phytoplankton degradation products (Herbland 1978). However, Herbland (1978) believed that in coastal and inland waters diverse origins were possible, including terrestrial detritus, phytoplankton, and phyto-benthic decay products. Loftus and Seliger (1975) suggested that, in low salinity water, soluble fluorescence was primarily an indicator of "humic acid-like" material. Carlson and Shapiro (1981) confirmed that dissolved humic substances are an important source of soluble fluorescence, at least in freshwater.

A major objective of the present investigation was to evaluate the use of F_{DCMU} as a measure of phytoplankton biomass at different salinities by testing the relationship between F_{DCMU} and extracted chlorophyll, before and after the subtraction of soluble fluorescence (S_{DCMU}). Other objectives were to compare measurements of soluble fluorescence with (S_{DCMU}) and without (S_{IVF}) the addition of DCMU, and to quantitatively explore the suggested link between soluble fluorescence and salinity. Although we do not identify the materials responsible for soluble fluorescence, dissolved humic compounds have been implicated by others (Loftus and Seliger 1975; Herbland 1978). Since humic compounds have a dominating influence on light availability (Kirk 1976), we examined the relationship between S_{DCMU} and light extinction coefficients as well.

Materials and Methods

Experimental Design

Data for the study were collected from natural plankton populations in four large-scale mesocosms (13 000 L, 5.0 m deep, for description see Oviatt et al. 1986) maintained at salinities of about 0, 5, 10, and 30 ppt. Additional data were obtained from Narragansett Bay at the Graduate School of Oceanography (GSO) dock station (~30 ppt) and along a salinity gradient in the Pawcatuck River, Rhode Island.

In early September 1987, four flow-through (480 $L \cdot d^{-1}$, 27-d turnover), well-mixed (2 h on, 4 h off), mesocosms at the Marine Ecosystems Research Laboratory (MERL) were established as independent (unconnected) systems with salinities of ~0, 5, 10, and 30 ppt. The initial salinities were achieved by introducing freshwater (from the Pawcatuck River) and/or seawater (from Narragansett Bay) in the necessary proportions to each tank. Sediment trays (0.96 m^3) containing intact benthic communities from low (3–20 ppt) or high (22–30 ppt) salinity stations along the Pawcatuck River estuary (Fig. 1) were placed in the bottom of mesocosms matching that of each community's origin.

From September to December 1987 each mesocosm was supplied with freshwater and/or seawater from the above sources at the required rate to maintain the selected salinities. For the final three weeks of the experiment, mesocosms were interconnected. Freshwater was introduced at one end of the series of tanks and seawater at the other; air driven displacement pumps transferred water between tanks, with low salinity water added at the surface and high salinity water added at depth (for additional details, see Klos 1988).

Sampling

A survey of the Pawcatuck River estuary, the freshwater source, was conducted on 30 October 1987. Samples for the analysis of chlorophyll *a*, IVF, F_{DCMU}, soluble fluorescence, and salinity were collected at six stations along the estuary (Fig. 1). Light extinction coefficients were also determined at each station.

River water from the 0 ppt salinity station was delivered to MERL every 2–3 wk (20 m^3 shipments) and stored in two mesocosms which served as freshwater reservoirs. The freshwater reservoirs, the four experimental mesocosms, and Narragansett Bay at the GSO dock were sampled regularly throughout the study.

IVF, F_{DCMU}, and soluble fluorescence with (S_{DCMU}) and without (S_{IVF}) DCMU were measured daily in each mesocosm (including the freshwater source mesocosm) and Narragansett Bay from 22 September to 31 December 1987. Extracted chlorophyll *a*, salinity and light extinction coefficients (27 October–31 December) were determined at weekly intervals.

Analytical Methods

To ensure similarity of light history effects, in vivo chlorophyll fluorescence was measured from pooled water samples collected from 0.1, 0.5, and 4.5 m depths in each mesocosm and Narragansett Bay at the same time each day (0900–1000). Samples were taken from the four treatment mesocosms during the morning mixing period; the freshwater source mesocosm was unmixed. Samples were siphoned through 1-cm diameter black polyethylene tubing into amber polyethylene bottles and read within 1 h (allowing at least a 10-min dark adaptation period: Vincent 1981; Falkowski and Kiefer 1985).

IVF, F_{DCMU}, S_{IVF}, and S_{DCMU} were measured with a Turner Design Model 10 Field Fluorometer equipped for chlorophyll *a* analysis. The fluorometer used a red-sensitive photomultiplier and the filter and lamp recommended by the manufacturer (blue lamp; excitation filter, Corning 5-60; reference filter, Corning 3-66; emission filter, Corning 2-64).

After gentle shaking, about 10 ml of sample were added to two separate 1-cm glass cuvettes, one for measuring IVF and the other for DCMU-enhanced measurements. Two drops of saturated DCMU (Lambert and Oviatt 1986) were added to the second cuvette (inverted twice to mix) for a final concentration of approximately 10^{-5} M. For soluble fluorescence (S_{IVF} and S_{DCMU}) the above procedure was repeated using 10 ml of 1.0 μm filtered sample (Whatman GF/F).

To account for instrument drift, basic fluorescence procedures were modified (Donaghay, pers. comm.) by reading a coproporphyrin standard (Sigma Chemical Co., St. Louis, MO) after each fluorescence measurement. The standard solution was prepared by dissolving coproporphyrin in 0.1 N HCl to a final concentration of 0.14 $\mu g \cdot mL^{-1}$ (DeManche 1979). Standards were flame sealed in 1-cm glass cuvettes and stored in the dark when not in use.

Using the same fluorometer, replicate values for extracted chlorophyll *a* ($mg \cdot m^{-3}$) were measured weekly from 10 ml aliquots of the pooled samples. The technique used was that of Yentsch and Menzel (1963) as modified by Lorenzen (1966) and described by Strickland and Parsons (1972). Samples were

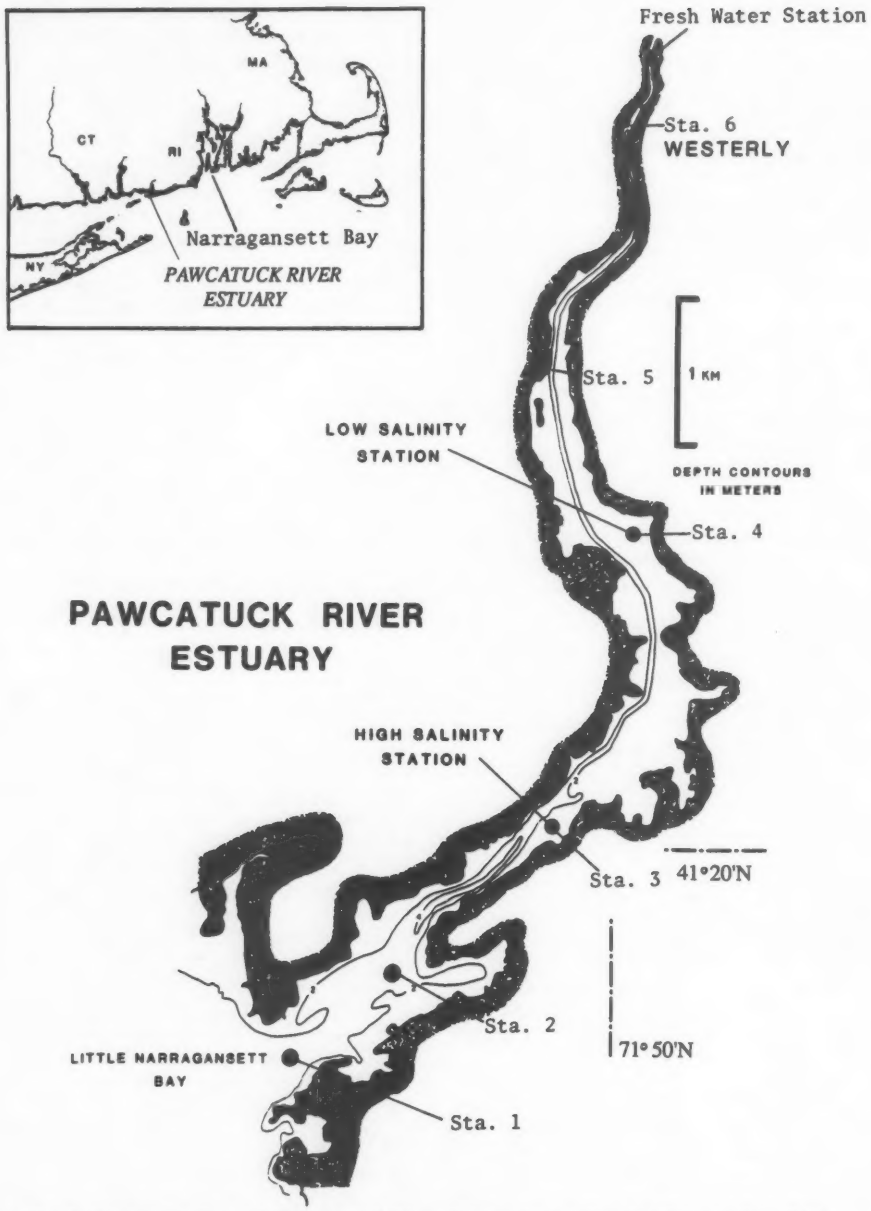

FIG. 1. Narragansett Bay and the Pawcatuck River, showing the location of sediment stations (high- and low-salinity stations) and freshwater-source station, as well as the sampling sites (stations 1–6) along the estuary for the 30 October 1987 river survey. Figure drawn by E. Klos.

filtered onto Whatman 25 mm GF/F glass fiber filters (1-μm particle retention), frozen and extracted within 2 wk using 90% acetone. Coproporphyrin standards were again read after each measurement. Chlorophyll measurements were periodically tested for the presence of chlorophyll *b* using a Beckman Model 26 spectrophotometer (Strickland and Parsons 1972). Since concentrations of chlorophyll *b* were consistently low (<0.2 mg·m^{-3}) in all treatments, our results are reported as chlorophyll *a*.

Extinction Coefficients and Salinity

Available light at depths of 0.1, 0.5, 1.0, 2.5, and 4.5 m was measured using a cosine corrected LI-COR, LI-192S underwater quantum sensor coupled to a LI-185 quantum meter.

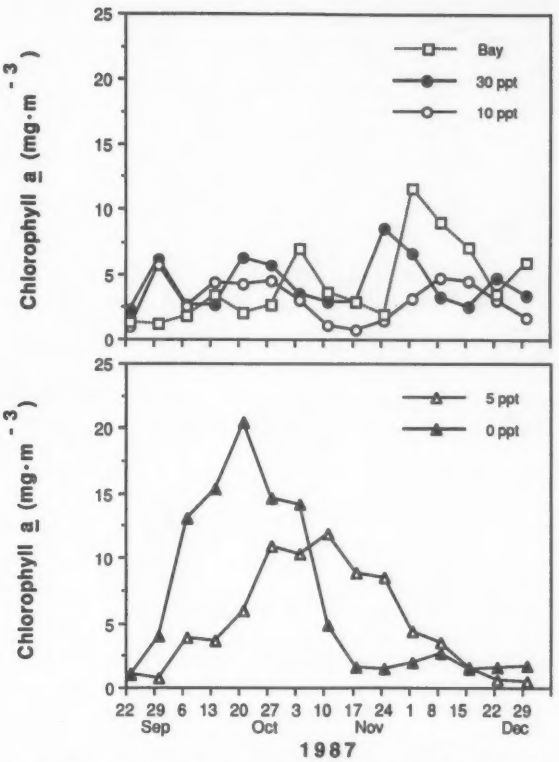

FIG. 2. Weekly concentrations of chlorophyll *a* ($mg \cdot m^{-3}$) from (a) Narragansett Bay (open squares) and the 10 ppt (open circles) and 30 ppt (closed circles) treatment mesocosms and (b) the 0 ppt (closed triangles) and 5 ppt (open triangles) treatment mesocosms over the experimental period, 22 September–31 December 1987.

Light profile data were fit to the exponential model for decay of light with depth.

(1) $I_z = I_0 \exp(-kz)$

where k (m^{-1}) is the extinction coefficient, I_z (einstein$\cdot m^{-2} \cdot s^{-1}$) is photosynthetically available radiation, PAR, at depths z (m) and I_0 is PAR at the surface, assuming a homogeneously mixed water column. Salinity (ppt) was monitored on a weekly basis with a Beckman induction salinometer.

Results

Time Series Measurements

Chlorophyll *a* concentrations in the 30 ppt treatment and Narragansett Bay (Fig. 2) were characterized by a series of small blooms (<10 $mg \cdot m^{-3}$) generally increasing in both duration and magnitude over the experimental period. Although the chlorophyll *a* concentrations were similar between the bay and the 30 ppt treatment, the timing of events was not synchronous. The 10 ppt treatment was similar to the high salinity systems in that chlorophyll *a* concentrations remained low (<10 $mg \cdot m^{-3}$) and exhibited a series of small blooms. In general, chlorophyll concentrations were somewhat lower in the 10 ppt treatment relative to the high salinity systems. The 5 ppt treatment showed a gradual increase in chlorophyll *a* level

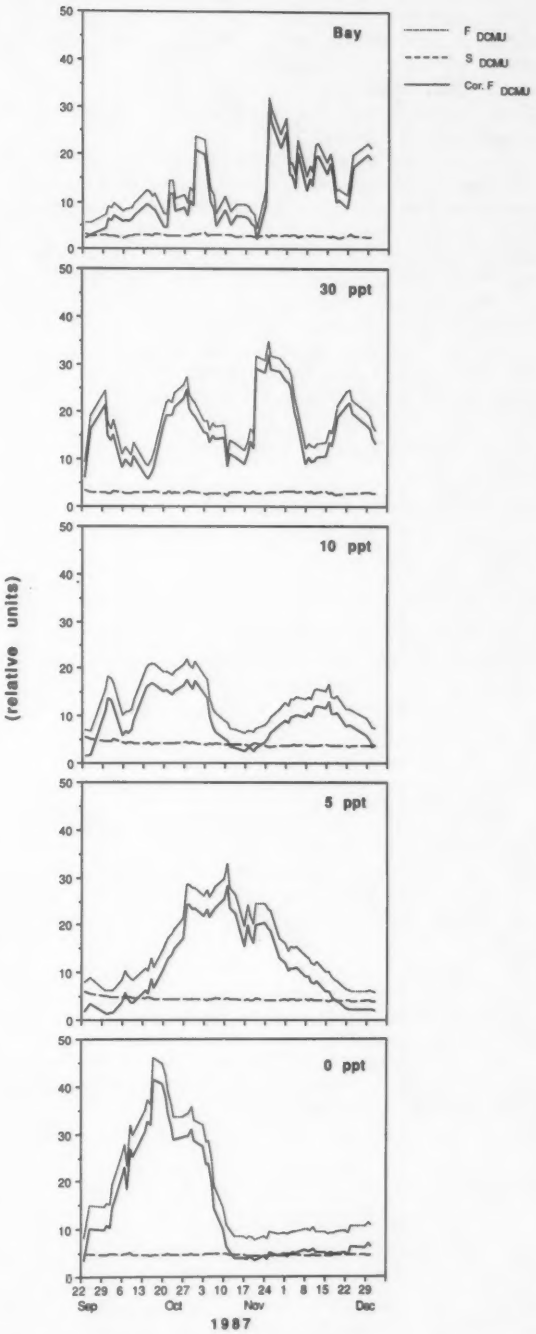

FIG. 3. Daily concentrations of F_{DCMU} (relative units) corrected (solid line) and uncorrected (dotted line) by subtraction of soluble DCMU-enhanced fluorescence (S_{DCMU}, dashed line) for (a) Narragansett Bay, (b) the 30 ppt mesocosm, (c) the 10 ppt mesocosm, (d) the 5 ppt mesocosm and (e) the 0 ppt mesocosm over the experimental period, 22 September–31 December 1987.

(Fig. 2) to a maximal value of ~12 $mg \cdot m^{-3}$ mid-way through the experiment (10 November), followed by a gradual decline. A similar pattern of increase in chlorophyll *a* was observed in the 0 ppt treatment (Fig. 2), although the peak concentration (~20 $mg \cdot m^{-3}$) was greater and occurred earlier in the experiment (20 October).

The daily fluorescence values (F_{DCMU}) confirmed the pattern of changing phytoplankton biomass observed with the less frequently measured (weekly) chlorophyll *a* concentrations (Fig. 3). The fluorescence figures also indicated that S_{DCMU} was relatively constant with treatment (although initially with a slight decreasing trend in the 5 and 10 ppt treatments). Soluble DCMU fluorescence contributed from 8–93% of the total DCMU-enhanced fluorescence. Correcting for S_{DCMU} (i.e. by subtraction) decreased the relative concentration of total F_{DCMU} but did not alter the overall pattern of change over the experimental period (September–December 1987).

IVF vs. DCMU-Enhanced Fluorescence

IVF and F_{DCMU} (uncorrected for soluble fluorescence) were significantly ($P<0.001$) and positively related (Model II linear regression, Laws and Archie 1981) throughout the experimental period.

$$(2)\quad F_{DCMU} = -4.84\ (\pm 0.34) + 2.54\ (\pm 0.04)\ IVF$$

with $r^2 = 0.91$ and $n = 385$ (values in parentheses are standard errors). F_{DCMU} and IVF were similarly related after correction for S_{DCMU} and S_{IVF} (not shown). Because of the close relationship between the two variables, results are generally presented only for F_{DCMU}.

DCMU-Enhanced Fluorescence vs. Chlorophyll *a*

To examine the relation between DCMU-enhanced fluorescence and chlorophyll *a*, with and without the presence of S_{DCMU}, regression equations were developed for each mesocosm and Narragansett Bay. Initially, uncorrected values of F_{DCMU} (i.e. without subtraction of soluble DCMU fluorescence) were regressed (Model II linear regressions) against chlorophyll *a* (Table 1). Among all mesocosms and the bay, F_{DCMU} and Chl *a* were significantly related ($P<0.001$) and a large percentage (84–99%) of the variation in F_{DCMU} was correlated with Chl *a*, even in the highly colored freshwater mesocosm and its source tanks. The intercepts of the regression equations (Table 1) were significantly different from zero and increased with decreasing salinity.

When corrected values of F_{DCMU} (i.e. after subtraction of S_{DCMU}) were similarly regressed against chlorophyll *a*, a second set of equations was generated (Table 2). The developed relationships were again all highly significant. Moreover, the coefficients of determination between F_{DCMU} and Chl *a* remained the same. The slopes of the regression equations for each treatment also did not significantly change after correction for S_{DCMU} (Tables 1 and 2). Intercepts for the second set of equations were now, however, no longer significantly different from zero.

Examination of the regression equations (Table 2) suggested that pooling between some treatments was possible. Based on analysis of covariance testing for homogeneity of regressions, (SAS 1981) there were no significant differences ($P>0.05$) in regression equations between the bay, 30 ppt and 10 ppt treatments, the 10 and 5 ppt treatments, and the freshwater treatment and its source mesocosms. Data from treatments with no significant differences were combined yielding three subgroups. The regressions between corrected F_{DCMU} and Chl *a* were subsequently calculated for each subgroup, pooling the 10 with the 5 ppt treatment rather than with the 30 ppt treatment (Fig. 4). For the high salinity treatments (bay and 30 ppt), the coefficient of determination indicated that 84% of the variation in F_{DCMU} could be explained by changes in chlorophyll *a* concentration. For the 5 and 10 ppt treatments, 88% of the variation was explained and for the freshwater mesocosms, 95%. The slopes of the pooled regression equations decreased with decreasing salinity (Fig. 4).

The Pawcatuck River data (30 Oct.) were handled in a similar fashion. F_{DCMU} (corrected and uncorrected for S_{DCMU}) was regressed against Chl *a* for six stations at varying salinities. Positive linear relationships (Model II) were observed (Tables 1, 2) with no significant difference in slopes between the two regressions. Again, a significant positive intercept before correction for S_{DCMU} was not different from zero after subtraction.

Soluble IVF vs. Soluble DCMU-Enhanced Fluorescence

Soluble fluorescence by definition is fluorescence which is not associated with a functioning photosynthetic system. The choice of a 1-μm (particle retention) filter, however, was based on the accepted filter size used in extracted chlorophyll *a* analyses (see methods). The occurrence of photosynthetic organisms in the <1-μm fraction was examined by comparing soluble fluorescence in the filtrate with and without the addition of DCMU for the mesocosms, Narragansett Bay, and the Pawcatuck River (Fig. 5). If no photosynthetic organisms were pre-

TABLE 1. Linear regression analyses (Model II) of uncorrected F_{DCMU} (without subtraction of S_{DCMU}, relative units) vs. chlorophyll *a* ($mg \cdot m^{-3}$) for individual mesocosms, Narragansett Bay, and the Pawcatuck River.

		Regression equation: $F_{DCMU} = m\ chl\ a + b$			
Tank	Treatment	m(± SE)	b(± SE)	r^2	*N*
6, 8	Freshwater source	1.38 (0.06)	6.87 (0.51)	0.98	15
9	0 ppt	1.78 (0.08)	5.99 (0.71)	0.98	15
7	5 ppt	2.23 (0.09)	4.47 (0.57)	0.98	15
5	10 ppt	3.16 (0.48)	3.54 (1.64)	0.70	15
3	30 ppt	4.05 (0.41)	1.45 (1.91)	0.87	15
	Narragansett Bay	3.05 (0.20)	1.30 (0.80)	0.95	13
	Pawcatuck River	1.93 (0.44)	5.07 (1.80)	0.89	13

TABLE 2. Linear regression analyses (Model II) of corrected F_{DCMU} (with subtraction of S_{DCMU}, relative units) vs. chlorophyll *a* ($mg \cdot m^{-3}$) for individual mesocosms, Narragansett Bay, and the Pawcatuck River.

		Regression equation: $F_{DCMU} = m \text{ chl } a + b$			
Tank	Treatment	m(±SE)	b(±SE)	r^2	*N*
6, 8	Freshwater source	1.41 (0.07)	1.49 (0.58)	0.97	15
9	0 ppt	1.78 (0.08)	1.46 (0.72)	0.98	15
7	5 ppt	2.26 (0.10)	−0.04 (0.63)	0.98	15
5	10 ppt	3.18 (0.48)	−0.42 (1.66)	0.69	15
3	30 ppt	4.04 (0.41)	−1.24 (1.94)	0.86	15
	Narragansett Bay	3.03 (0.20)	−1.36 (0.78)	0.95	13
	Pawcatuck River	1.89 (0.43)	1.12 (1.78)	0.85	13

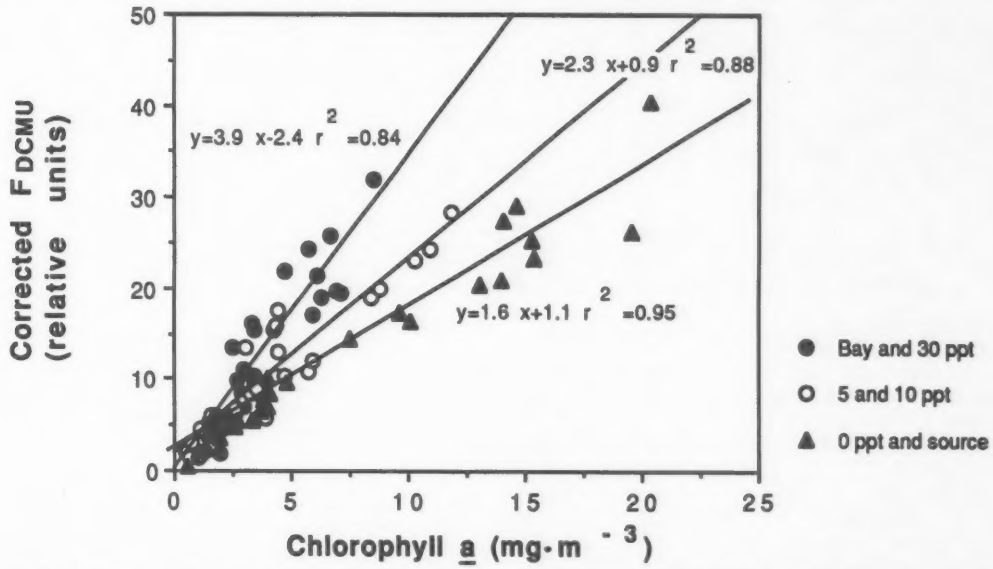
Corrected F DCMU (relative units)
Chlorophyll a (mg·m⁻³)
y=3.9 x-2.4 r² =0.84
y=2.3 x+0.9 r² =0.88
y=1.6 x+1.1 r² =0.95
Bay and 30 ppt
5 and 10 ppt
0 ppt and source

FIG. 4. Relation between DCMU-enhanced fluorescence (F_{DCMU}, relative units), corrected for S_{DCMU} and extracted chlorophyll *a* ($mg \cdot m^{-3}$) for Narragansett Bay and the 30 ppt treatment (closed circles), the 5 and 10 ppt treatments (open circles) and the 0 ppt treatment and the freshwater source mesocosms (closed triangles) over the experimental period.

sent, soluble fluorescence would be insensitive to the addition of DCMU and all the points in Fig. 5 would fall along the 1:1 line. S_{DCMU}, however, was always greater than S_{IVF}. The ratio for each pair of soluble fluorescence values (with and without DCMU) was subsequently calculated by dividing S_{DCMU} by S_{IVF}. Ratios ranged from 1.02 to 1.80 with a mean of 1.20 (±0.01, SE, $n = 392$) and increased with salinity (0 ppt = 1.11, 5 ppt = 1.13, 10 ppt = 1.18, 30 ppt = 1.35). On average, 83% of the fluorescence in the <1-μm fraction was attributed to dissolved substances.

Soluble DCMU-Enhanced Fluorescence vs. Salinity

In general, S_{DCMU} (shown) and S_{IVF} (not shown) decreased with increasing salinity (Fig. 6, representative plots of S_{DCMU} vs. salinity from the beginning, middle, and end of the experimental period). During the early weeks, S_{DCMU} fluorescence was lower in the 0 ppt treatment compared with both the freshwater source mesocosm at the start of the experiment and the 5 ppt salinity treatment. For the remainder of the experiment, there were slight deviations from a linear relationship which suggested a loss or removal of S_{DCMU} along the experimental salinity gradient. Recall that, prior to December, mesocosms were connected only to the freshwater source mesocosm and the bay and not connected to each other. The asymmetry in the S_{DCMU} vs. salinity relationship consistently increased after the mesocosms were connected (based on 3 wk of data as represented by December in Fig. 6). A similar relationship was found between S_{DCMU} and salinity for the Pawcatuck River data (Fig. 7). Again S_{DCMU} decreased with increasing salinity with the asymmetry in the relationship, indicative of the loss of soluble fluorescent material along the increasing salinity gradient.

Despite the asymmetry in the above relations, a highly significant ($P < 0.001$) inverse relationship (Model II) was observed between S_{DCMU} and salinity for all treatments over the experimental period:

$$(3) \quad S_{DCMU} = 4.57\ (\pm 0.02) - 0.060\ (\pm 0.001)\ \text{Salinity}$$

with $r^2 = 0.88$ and $n = 90$ (values in parentheses are standard errors). A similar relation was noted for S_{IVF} vs. salinity (not shown).

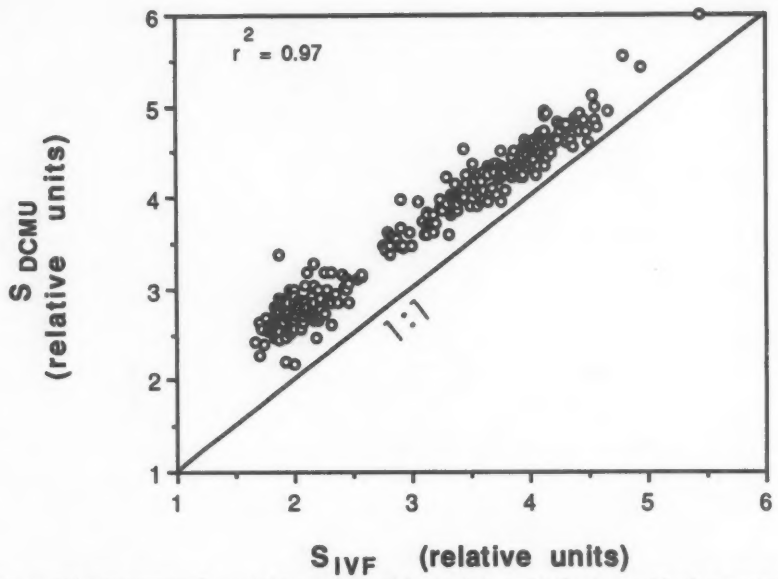

FIG. 5. Relation between S_{DCMU} (relative units) and S_{IVF} (relative units) for the combined mesocosms, Narragansett Bay (22 September–31 December 1987), and the Pawcatuck River (30 October 1987). The diagonal line represents the 1:1 relation between variables.

Light Extinction vs Soluble DCMU-Enhanced Fluorescence

Light extinction coefficients and S_{DCMU} were positively related (Model II, $P<0.001$) for the four salinity treatments from 27 October–31 December 1987 (Fig. 8). A significant linear relationship was also found between light extinction coefficients and S_{DCMU} for the Pawcatuck River stations on 30 October (not shown). For the mesocosms, the coefficient of determination indicated that 74% of the variation in light extinction could be explained by changes in S_{DCMU}; the coefficient of determination for the Pawcatuck River was 0.96. There were no significant differences ($P>0.05$) between the linear regressions for the mesocosms and the Pawcatuck River. Similar results were found for k vs. S_{IVF} ($r^2=0.74$ mesocosms; $r^2=0.96$ river).

Discussion

Rapid and reliable methods for measuring phytoplankton biomass (and/or primary production) are desirable, particularly to increase the spatial and temporal coverage of heterogeneous environments. Frequently, the search for less time-consuming methods has led to the use of in vivo fluorescence techniques (Owens et al. 1980; Bates and Platt 1984). Our research demonstrated that to accurately estimate chlorophyll using in vivo fluorescence along an estuarine salinity gradient it is essential to correct for soluble fluorescence (by subtraction). Even with the added constraint of measuring S_{DCMU}, analysis of in vivo fluorescence remains less labor-intensive than measurement of extracted chlorophyll *a*.

Correcting for S_{DCMU} did not reduce the variability in the DCMU-enhanced fluorescence to extracted chlorophyll *a* relationship (as indicated by the coefficients of determination, Tables 1, 2). Moreover, for both the mesocosms and the Pawcatuck River, there were no significant differences ($P>0.05$) in the slopes of the regressions for each treatment before vs. after corrections for soluble fluorescence. The major change in the regression equations was a shift from positive intercepts which decreased with increasing salinity, to intercepts which were not significantly different from zero ($P>0.05$) for all treatments.

These results contrast with those of Carlson and Shapiro (1981). They found a significant improvement in the IVF:Chl *a* relation after adjusting for soluble fluorescence in freshwater lakes. The contrasting results may be related to the systems sampled. Carlson and Shapiro (1981) sampled 22 lakes over a wide geographic range, while our results are representative of a single estuarine system. Both studies indicated that, when using in vivo fluorescence techniques alone, correcting for soluble fluorescence is essential to avoid overestimating phytoplankton biomass. Our research demonstrated that S_{DCMU} was relatively constant at a given salinity and unrelated to total DCMU-enhanced fluorescence. Soluble DCMU-induced fluorescence (i.e. S_{DCMU}-S_{IVF}) was also unrelated to F_{DCMU} over the experimental period. It thus becomes increasingly important to correct for soluble fluorescence along an estuarine salinity gradient during periods of low phytoplankton biomass.

Our results further indicated that a single linear regression between DCMU-enhanced fluorescence and chlorophyll *a* was inappropriate for the ranges of salinities encountered in the study. The regression equations were significantly different between high and low salinity treatments regardless of adjustments for S_{DCMU}. As noted in the introduction, such differences have previously been attributed to species composition, size class, nutrient stress, and diel periodicities.

DCMU, a metabolic inhibitor, acts by blocking non-cyclic photosynthetic electron transport and eliminates the quenching of fluorescence by active Photosystem II (PS II) reaction centers (Papageorgiou 1975; Samuelsson and Öquist 1977; Slovacek and Hannon 1977; Falkowski and Kiefer 1985). The

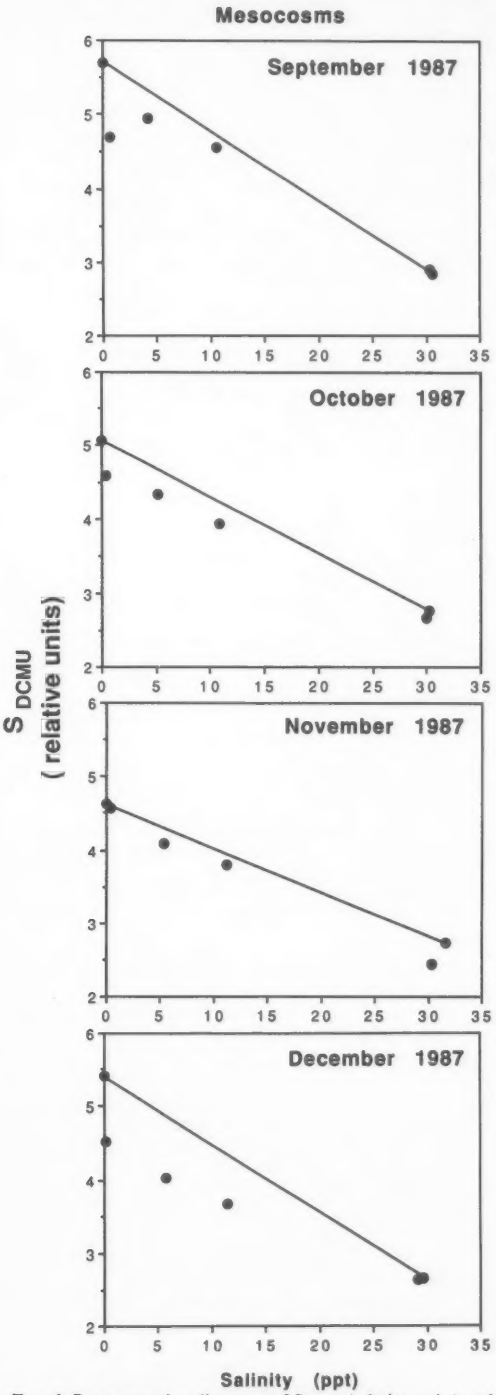

FIG. 6. Representative diagrams of S_{DCMU} (relative units) and salinity (ppt) during each month of the experiment. Mesocosms were unconnected prior to the December measurements. Diagonal lines join the freshwater-source mesocosm (from the Pawcatuck River) and the saltwater source (Narragansett Bay).

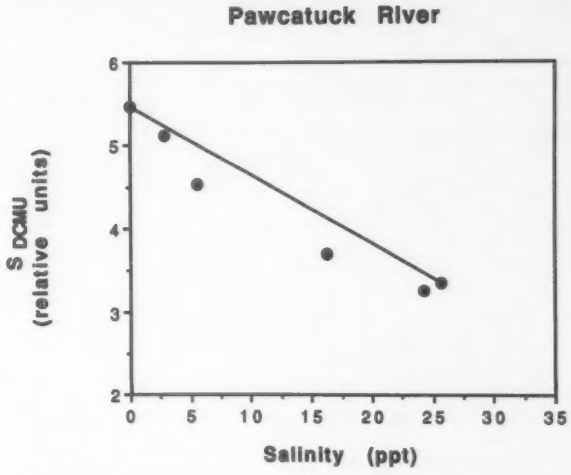

FIG. 7. S_{DCMU} (relative units) vs. salinity (ppt) for the Pawcatuck River measurements (30 October 1987). Diagonal line connects the low- and high-salinity stations to demonstrate the removal of S_{DCMU} along the salinity gradient.

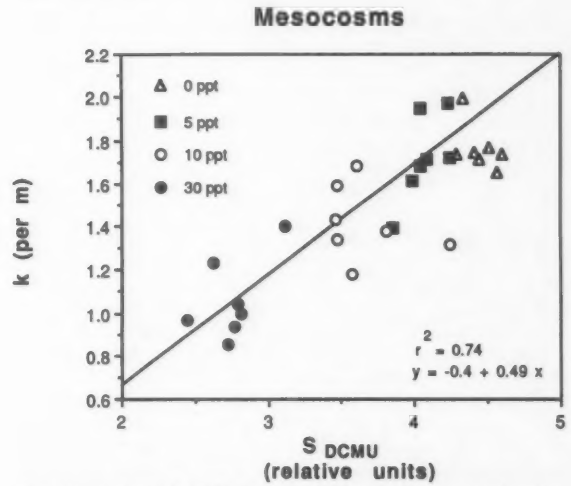

FIG. 8. Relation (Model II, linear regression) between vertical extinction coefficients (k, per m) and S_{DCMU} (relative units) for the 0, 5, 10, and 30 ppt treatments (27 October–31 December 1987).

increase in soluble fluorescence with the addition of DCMU indicated that a portion of the fluorescence in the <1-μm size fraction was associated with an active PS II. For both the mesocosm and the field data, an average of 17% (range 2–78%) of the fluorescence in the <1-μm filtrate was due to intact cells and therefore was not strictly soluble fluorescence. The presence of very small intact cells in the filtrate, however, will not affect the corrected DCMU-enhanced fluorescence to extracted chlorophyll *a* relationship provided precautions are taken to use the same volume of water and filter-size in both analyses. Yentsch (1983) similarly noted the presence of very small organisms with photosynthetic capabilities in glass-fiber filtrate.

In the low-salinity waters of the upper Chesapeake Bay, Loftus and Seliger (1975) observed soluble fluorescence values

greater than 50% of the total, while lower percentages (<10%) were found in the high-salinity bay proper. Tunzi et al. (1974) similarly noted that soluble fluorescence was greater in the upper part of San Francisco Bay near the Guadulupe Slough with decreasing values in the lower bay. Alpine and Cloern (1985), also working in San Francisco Bay, reported soluble fluorescence values ranging from 7–76% of total IVF. For freshwater lakes, Carlson and Shapiro (1981) observed that soluble fluorescence contributed from 14–100% of the total fluorescence, while for high-salinity, oceanic regions Herbland (1978) reported that soluble fluorescence ranged from 10–60% of total IVF. Comparable results were found in the current analysis. An average of 32% of the total DCMU-enhanced fluorescence (range 8–93%) was present in the <1-μm filtrate and interpreted as the soluble fraction.

Soluble fluorescence was significantly related to salinity throughout the experimental period. The inverse relationship between S_{DCMU} and salinity in the mesocosms and the field confirmed the qualitative results suggested by earlier studies (Tunzi et al. 1974; Loftus and Seliger 1975; Herbland 1978). Mixing diagrams (Fig. 7) for individual sample periods generally exhibited decreased fluorescence with increasing salinity. The comparatively low soluble fluorescence in the 0 ppt mesocosm at the start of the experiment most likely resulted from different levels of soluble fluorescence (unmeasured) in the Pawcatuck River water initially used to fill the individual mesocosms.

The Pawcatuck River measurements clearly indicated that S_{DCMU} did not behave in a conservative fashion along the salinity gradient. Some loss of the material responsible for soluble fluorescence occurred. A similar pattern was observed in the mesocosms, with the removal enhanced after the mesocosms were connected. Carlson and Shapiro (1981) demonstrated that in lake waters, dissolved humic substances were primarily responsible for soluble fluorescence. Our results suggest that these materials are removed to some extent within the estuary, perhaps by adsorption onto particulate matter followed by precipitation, and/or biologically mediated uptake. The observed variation in the ratio of S_{DCMU} to S_{IVF} with salinity is consistent with the dilution, coupled with removal, of the humic component along the salinity gradient.

The effect of "yellow substance" or Gelbstoff (composed chiefly of fulvic and humic acids) on attenuation of photosynthetically active radiation in inland and coastal waters has been documented (Kirk 1977b). Kirk (1976, 1977b) noted that vertical attenuation coefficients increased with increasing concentrations of Gelbstoff. For the range of extinction coefficients observed in the current study, Kirk's (1976) findings were linear. In addition to Gelbstoff, extinction coefficients have previously been correlated with increasing levels of phytoplankton biomass (Riley 1975) and/or particulate matter (Kirk 1977a; Campbell and Spinrad 1987).

Our observations demonstrated a significant linear relation between light attenuation and S_{DCMU}, both in the mesocosms and the Pawcatuck River. However, attenuation of light was not significantly related to chlorophyll *a* concentration and inorganic suspended matter was unmeasured. The observed correlation between light extinction and soluble fluorescence, together with the prior findings of Carlson and Shapiro (1981), suggests to us that humic materials are the most likely source of soluble fluorescence along the salinity gradient.

In conclusion, we have shown that DCMU-enhanced fluorescence and extracted chlorophyll *a* are highly correlated both before and after correction for soluble fluorescence. Correcting for soluble fluorescence (by subtraction) is essential, particularly during periods of low phytoplankton biomass, to accurately estimate in vivo chlorophyll using fluorescence techniques in estuarine waters. Additionally, soluble DCMU-enhanced fluorescence, decreased along an increasing estuarine salinity gradient (as a result of dilution coupled with removal), is significantly related to both salinity and light extinction and is primarily non-photosynthetic material. Finally, the relationships demonstrated throughout the manuscript were consistent between the mesocosms and the field data.

Acknowledgements

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Distribution of Shrimp and Fish By-Catch Assemblages in the Canadian Eastern Arctic in Relation to Water Circulation

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Hudon, C. 1990. Distribution of shrimp and fish by-catch assemblages in the Canadian eastern Arctic in relation to water circulation. Can. J. Fish. Aquat. Sci. 47: 1710–1723.

In the Canadian eastern Arctic, the catches of common species of decapods and fish in bottom trawls reveal a continuum of increasing species richness and abundance in an easterly direction through Hudson Strait. Species richness is greatest in Ungava Bay, where Arctic and Labrador Sea components of the fauna coexist. Over the study area, species could be divided in three associations corresponding to the origin of the predominant water masses: Arctic cod, cottids, zoarcids, and liparids predominate in the Arctic waters of western and central Hudson Strait; Greenland halibut, roughhead grenadier, and three-beard rockling are characteristic of the northern Labrador Sea; pandalid shrimp are abundant in areas of deep (> 300 m), intensely mixed waters near the mouth of Hudson Strait. Pink shrimp (*Pandalus borealis*) predominates in Davis Strait–Labrador Sea, whereas it is replaced by the striped pink shrimp (*P. montagui*) in eastern Hudson Strait, reflecting environmental optima in subarctic and Arctic dominated waters, respectively. The yearly catches of striped pink shrimp are highly variable, possibly related to mixing intensity in eastern Hudson Strait. In Canadian Arctic waters, species richness, distribution, and abundance are related to temperature, salinity, mixing, and general circulation of water masses.

La richesse et l'abondance des captures de décapodes et de poissons dans les chaluts de fond dans l'arctique oriental canadien suivent un gradient croissant dans l'axe ouest-est du Détroit d'Hudson. La richesse en espèce est maximale dans la Baie d'Ungava, ou coexistent des composantes de la faune arctique et de la Mer du Labrador. Dans la région d'étude, les espèces peuvent être divisées en trois associations correspondant au degré d'influence des principales masses d'eaux. La morue arctique, les cottidés, les zoarcidés et les liparidés prédominent dans les eaux à l'ouest et au centre du Détroit d'Hudson; le flétan du Groenland, le grenadier et la mustèle arctique à trois barbillons sont caractéristiques de la Mer du Labrador; les crevettes abondent dans les eaux profondes (> 300m), fortement mélangées près de l'embouchure du détroit. La crevette rose (*Pandalus borealis*) prédomine dans le détroit de Davis et la Mer du Labrador, et est remplacée par la crevette ésope (*P. montagui*) à l'est du détroit d'Hudson, reflétant un optimum environnemental dans les eaux à dominance subarctiques et arctiques, respectivement. Les captures annuelles de crevette ésope varient beaucoup, possiblement en relation avec l'intensité du mélange dans l'est du Détroit d'Hudson. Dans l'arctique oriental canadien, la richesse spécifique, leur distribution et leur abondance sont reliées à la température, à la salinité, au mélange et à la circulation générale des masses d'eaux.

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Fisheries resources of Hudson Strait and Ungava Bay are poorly known, especially in deeper waters, and until recently the offshore resources were not exploited. Early accounts of the fishes of Ungava Bay (Dunbar and Hildebrand 1952) and Labrador (Backus 1957) listed species commonly found in those areas, but did not evaluate the potential for commercial exploitation. Fisheries surveys carried out in later years (see Table 1) revealed high concentrations of striped pink shrimp (*Pandalus montagui*) west of Resolution Island (eastern Hudson Strait) and in northeastern Ungava Bay (Veitch et al. 1981; Parsons et al. 1981). The species is also found off the west coast of Greenland, Labrador, Newfoundland (Squires 1965), and in the Gulf of St. Lawrence south to Cape Cod (Simpson et al. 1970).

In contrast with Hudson Strait and Ungava Bay, the adjacent areas of Davis Strait (NAFO Division 0B) – Labrador Sea (NAFO Division 2G) support a developing fishery for the pink or northern shrimp (*Pandalus borealis*), a circumboreal species, found in both the Atlantic and the Pacific Oceans. In the northwest Atlantic, it occurs from around 75°N off West Greenland to 42° off Georges Bank (Squires 1965, 1966), and is commercially exploited in the Gulf of St. Lawrence, off the coast of Labrador, and in Davis Strait.

Although both pandalids occur in the same geographical range, they are not found in the same water masses: *Pandalus borealis* is found in the deeper, warmer water, while *P. montagui* is found in shallower, colder water. The former is generally the more abundant species, except west of the mouth of Hudson Strait, where the striped pink shrimp is dominant. This well-defined change reflects the existence of a sharp environmental gradient between Davis Strait–Labrador Sea and Hudson Strait waters. In addition, such a marked change in physical conditions might result in changes in the fish species assemblage associated with the shrimp. The animal community could therefore serve as an indicator of the origins of the different water masses meeting and mixing in this large area.

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TABLE 1. Summary of the information on the ships surveyed. WHS: Western Hudson Strait and Northern Hudson Bay (74°00–82°00W); CHS: Central Hudson Strait (69°30–74°00W); EHS: Eastern Hudson Strait (64°40–69°30W); UB: Ungava Bay (south of 61°05N); RI: Resolution Island; 0B + 2G: NAFO Divisions 0B–Southern Davis Strait and 2G–Northern Labrador Sea.

Ship	Dates of survey	Type of trawl	Number of sets in region						Reference
			WHS	CHS	EHS	UB	RI	0B + 2G	
Canso Condor	Aug. 3–29, 1978	Sputnik 1600	—	—	8	10	—	50	MacLaren Marex 1978
Torsbugvin	Aug. 15–Oct. 5, 1979	Sputnik 1600	—	—	17	103	71	—	Gillis, unpubl. data, pers. comm.[a]
Thalassa	Sept. 14–22, 1979	Lofoten Expl.	—	—	2	22	—	—	Allard 1980
Lumaaq	Sept. 28–Oct. 7, 1980	Sputnik 1800	—	16	—	5	22	—	Imaqpik Fisheries Inc. 1981
Gadus Atlantica	Sept. 11–26, 1982	Sputnik 1600	—	—	—	40	53	18	Parsons 1982
Ocean Prawns	Oct. 4–16, 1986	Shjervøy	—	—	—	17	37	—	Anonymous 1986
A. Needler	Aug. 15–Sept. 9, 1988	Sputnik 1600	—	—	—	—	27	—	Parsons, unpubl. data, pers. comm.[b]
Kinguk	Aug. 9–19, 1989	Shjervøy, Hopedale	65	40	—	—	—	—	Allard 1990
		Total:	65	56	27	197	210	68	

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The present study synthesizes information from eight research and/or commercial cruises that aimed at assessing shrimp and groundfish resources in Northern Hudson Bay, Hudson Strait, and Ungava Bay. Comparisons of species composition, abundance, and distribution were made with southern Davis Strait (NAFO Division 0B) and northern Labrador Sea (NAFO Division 2G), when those areas were fished by the same vessels. The density of commercially important species was mapped and year to year variability estimated. Their distribution and abundance were then related to relevant hydrographic and oceanographic information. The biology of most species of commercial interest, as well as their salinity and temperature tolerance, are fairly well known, allowing their use as indicators of water masses.

Description of the Study Area

The marine environment of eastern Canada is strongly influenced by interacting water masses from the Arctic Ocean and the central North Atlantic (Dunbar 1951; LeBlond et al. 1981). Cold, low-salinity water enters Baffin Bay from the Arctic Ocean and flows southward, forming the Baffin island current over the shelf off eastern Baffin Island (Fig. 1). On the opposite side of the Labrador Sea, the West Greenland Current, derived from mixed Arctic and Atlantic waters, flows northward. One branch of this warmer flow crosses Davis Strait and joins the Baffin Island Current.

In Hudson Strait, Arctic water from Hudson Bay and Foxe Basin flows eastward along the Quebec shore, while a mixture of Atlantic and Arctic waters from Davis Strait moves westward along the Baffin Island coast (Prinsenberg 1986, Fig. 1). At the eastern entrance to the strait, a crosschannel southward current merges with outflowing waters from Ungava Bay (Drinkwater 1986). The waters below 200 m in western Hudson Strait are mostly of Arctic origin. Temperatures are cold and nearly isothermal (<0°C; Drinkwater 1986). In the eastern portion of the strait, and in northeastern Ungava bay, there is an increase in both temperature and salinity at depths >200 m due to the influence of Labrador Sea water (Drinkwater 1986; Fig. 2). These deep waters are not subject to much seasonal variations (Schroeder 1963), and identify the major water masses and oceanic curents most likely to influence demersal organisms.

Water masses originating from the West Greenland Current, Baffin Island Current, and Arctic waters of Hudson Bay can be identified from their temperature and salinity (T-S) curves (Fig.2). Overall, the waters within the Hudson Strait region constitute a continuum of T-S, from the characteristic Arctic water in the west (Fig.2, polygons 1–2) to the Labrador Sea water in the east (polygons 7–8). Ungava Bay water (polygon 4) is unique with T-S characteristics that overlap both Labrador Sea and northern Hudson Bay water; however, Ungava Bay contains warm, low salinity waters resulting from local river runoff (Dunbar 1951; Fig.2). A distinct water mass is found at the eastern entrance of Hudson Strait, formed by the converging and mixing of water from the Baffin Island Shelf, the low salinity outflow from Hudson bay and Foxe Basin, and offshore Labrador Sea water (Dunbar 1951; Fig.2).

During the summer, the degree of vertical density stratification in Hudson Strait and Ungava Bay varies spatially. Maximum stratification occurs along the Quebec side due to the advection of the low salinity surface water from Hudson Bay. Intense tidal mixing occurs in Ungava Bay and frontal areas have been observed across the mouth of Ungava Bay, across the eastern entrance of the Strait and around the southeastern tip of Baffin Island (Drinkwater and Jones 1987). The latter two areas also have high surface nutrients and phytoplankton biomass. Mixing in eastern Hudson Strait may enhance nutrient flux on the Labrador Shelf, with important biological consequences (Sutcliffe et al. 1983).

Methods and Statistical Analyses

Detailed set and catch data were obtained from the cruise reports of eight vessels operating in northern Hudson Bay, Hudson Strait, and Ungava Bay (Table 1). Set data include the date, time, position, duration, depth, and set type (research, commercial). Catch data include the weight (kg) of each species of decapod and fish caught during each set, standardized for a 0.5 h tow. The sets were divided among regions corresponding to western, central, eastern Hudson Strait, Ungava Bay, and 0B + 2G (Fig.1, Table 1). One additional region was delineated for shrimp fishing grounds west of Resolution Island (eastern Hudson Strait). Instead of the traditionally used oblique boundary from headland to headland, the northern boundary of

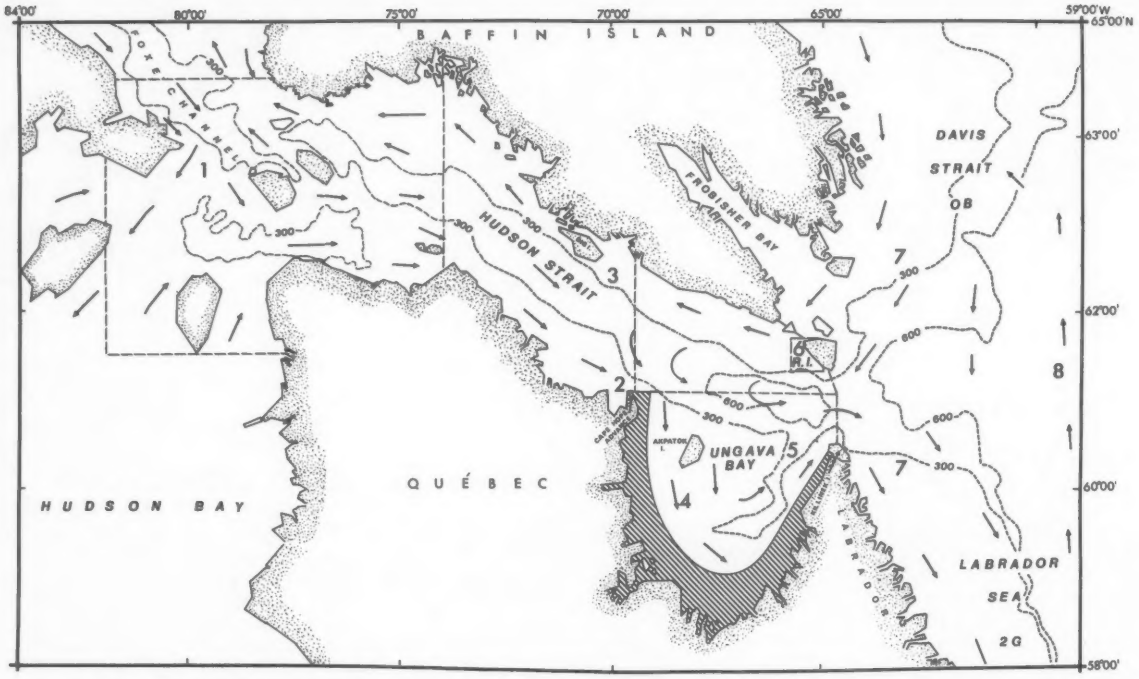

FIG. 1. Bathymetry (300 and 600 m isobaths) and general circulation (arrows, from Drinkwater (1986) and Prinsenberg (1986)) in the study area. Numbers correspond to T-S diagrams identified in Fig. 2 and indicate the general location of hydrographic stations. The shallow (<100 m) coastal zone of Ungava Bay (hatched), to which demersal fish distribution could not be extrapolated, was not included in the mapping of species distribution. Enclosed areas for Resolution Island (R. I.) and Ungava Bay are examined in detail in Figs. 3–5.

Ungava Bay was set at 61°05′ latitude, to facilitate mapping and include the entire area where shrimp fishing occurs. The coastal area of Ungava Bay was excluded from the mapping to avoid extrapolating demersal fish distribution into the coastal zone (< 100 m), potentially under the influence of the large freshwater outflow (Dunbar and Hildebrand 1952).

Catch data for each region were used to derive information on (A) relative species frequency and (B) quantitative abundance of common decapods and fish. Relative species frequency allocated all species to one of four classes corresponding to: (0) absent; (1) rare (species observed once); (2) occasional (species observed < 10% of sets); (3) common (species observed >10% of sets). Relative species frequency observed in the six regions was used for a cluster analysis to determine the species of fish exhibiting similar patterns of occurrence over the territory. This was accomplished using an intermediate linkage clustering algorithm, with a threshold for linkage at the 0.75 level (i.e. groups were formed at the level at which their components shared 75% of information). The similarity matrix was calculated using Gower's coefficient modified for asymmetric data (Legendre and Legendre 1984), which excludes the double absence of any species in the calculation of species association. This procedure yielded inter-regional comparisons of species richness while reducing the bias induced by possible misidentification of rare species.

Quantitative abundance (kg·30 min standard tow^{-1}) of common species was calculated only with species occurring in >10% of the tows in each region. In some cases (multivariate analyses and average catch statistics) species had to be lumped together at the genus or family level. Abundance data were ln-transformed ($\ln(x+1)$) due to the large number of zero values. When more than one set was carried out in the same location (19 cases), the average catch was used for mapping.

In order to identify the origin of catch variability within regions, zones of homogeneous species composition and abundance were identified within the Resolution Island and Ungava Bay areas. This was carried out using a cluster analysis with a spatial constraint (BIOGEO), producing maps of homogeneous species composition and abundance for Resolution Island and Ungava Bay. The similarity matrix between each pair of sets was computed using Gower's (1971) similarity coefficient. The homogeneous zones were delimited using clustering with spatial contiguity constraint (Legendre 1987), computed from the Gower similarity matrix. The term "homogeneous zone" is used here to mean a region of space, made of adjacent (contiguous) stations that are also similar for the variables under study. In the first step, proportional-link linkage agglomerative clustering (50% connectedness level) was computed with a spatial contiguity constraint (Legendre and Legendre 1984). The groups obtained were then defined using a non-hierarchical "K-means" clustering, minimizing the within-group variance (MacQueen 1967), also with spatial contiguity constraint. Both programs used for these computations are part of the "R package" (Legendre 1985). Each of these homogeneous zones was then characterized in relation to the prevailing hydrographic conditions (spatial variability) as well as the identity of the ship and year of sampling (differences in performance and/or temporal variability).

The distribution of common species was mapped using the Symap™ package (Dougenik and Sheehan 1977), proceeding

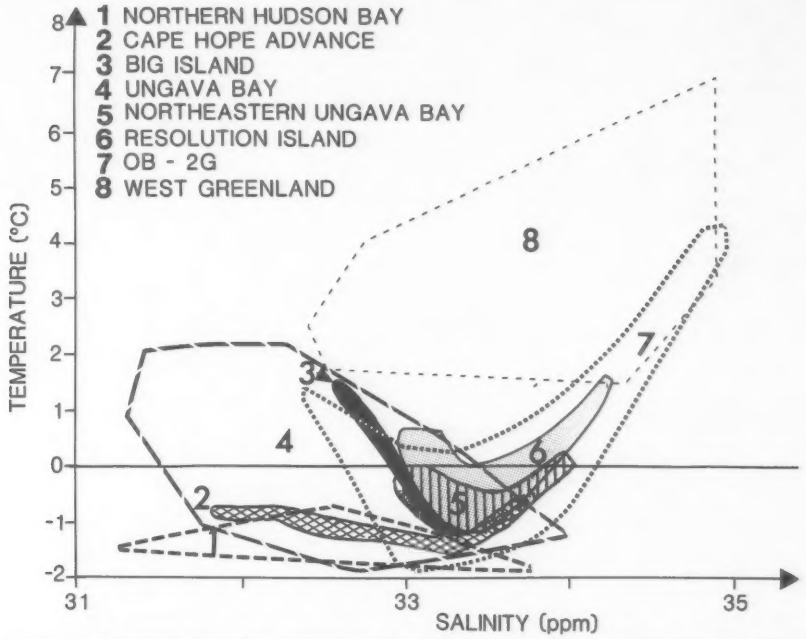

FIG. 2. T-S diagrams for various locations in the study area (see Fig. 1). Temperature and salinity values were taken at 50 m interval to the bottom, while omitting values from the surface to 50 m to eliminate the effect of seasonal variations. Hydrographic data were obtained from K. Drinkwater (Department of Fisheries and Oceans, BIO, C.P. 1006, Dartmouth, N.S. B2Y 4A2, pers. comm.: regions 1 and 7 (1982) region 4 (1986)); C. Hudon (unpubl. data: regions 2, 3, 5, 6 (1987)); Dunbar (1951: regions 4 and 8).

with the point distribution coefficient calculated by the nearest neighbour method (Clark and Evans 1954). The expected species density between two sampling points is calculated by interpolation, thus providing a map of the spatial distribution of any given species. The precision of the interpolation depends on the density of sampling stations. Mapping was not carried out for Hudson Strait (Fig. 1), due to low biomass of decapods and fish. The complete series of distribution maps of the most abundant species of fish and decapods for Resolution Island, Ungava Bay, and NAFO Division 0B and 2G can be found in Jarry (1988).

Fish associations were identified using a principal coordinate analysis (Legendre and Legendre 1984). In this analysis, the projection of the coordinates of each species on each of the first two principal coordinates axes is examined to determine which species account for most of the variability among sets. Species found in the same quadrat of the two-dimension space are associated. This analysis was carried out on the similarity matrix of fish abundance data while excluding catches of pandalid shrimps.

Finally, the affinity of the different regions with respect to their common species composition and abundance was determined using an intermediate linkage clustering algorithm (0.75 level). The similarity matrix of the average catch rates per standard tow unit was calculated on normalized data ($\ln(x+1)$) using Gower's (1971) similarity coefficient. This coefficient includes double absence in the calculation of the similarity coefficient between two regions. For example, the double absence of Myctophids in western and central Hudson Strait was taken as a similarity between the regions, rather than omitted from the calculation, as was the case with the analysis of frequency data.

Results

Relative Frequency of Fish and Decapod Species

Eighteen species of decapods and 58 species of fish were identified in the catches of the eight ships (Table 2). The degree of precision in specimen identification varied greatly from one ship to the next, sometimes being restricted to the family. Species reported only once and absent from adjacent areas could be attributed to either the depth range sampled, limits of geographical distribution, or misidentification. Although few specimens were kept for formal identification, most species were commonly caught in several sets by different ships operating in the same or adjacent areas (Table 2).

Ungava Bay exhibits a highly diversified decapod fauna (18 groups), more than twice the number reported in other areas (7–8 groups) (Table 3). For fish, Ungava Bay (51) and Resolution Island (48) support the largest number of groups (Table 3), although this could result from the heavier sampling effort in those two areas (Table 1). There is a gradient of increasing number of fish groups from the west to the east end of Hudson Strait. This gradient remains apparent even when rare species are not taken into account.

The cluster analysis on fish frequency data over the entire study area (Table 2) resulted in five groups of fish species (A–E) corresponding to specific geographic regions. Group A corresponds to species common in all regions, whereas groups

TABLE 2. List of fish and decapod species reported in each region. Frequency classes: 1, species recorded once; 2, species or group recorded for less than 10% of the sets; 3, species or group recorded for more than 10% of the sets. Regions are designated as in Table 1. * Specimen identification verified by D. McAllister (Museum of Natural History, Ottawa). (More recent taxonomic apellation). Gr.: Group to which each fish species was assigned by the cluster analysis of the regional pattern of abundance (see text).

			Frequency class in regions						
Common Name	Family/Genus	Species	WHS	CHS	EHS	UB	RI	0B	
Decapods									
Pink shrimp	*Pandalus*	*borealis*	2	2	2	2	2	3	
Striped pink shrimp	*Pandalus*	*montagui*	3	3	2	3	3	2	
	Lebbeus	*polaris*	2	1	2	2	2	2	
	Lebbeus	*groenlandicus*				2			
	Lebbeus	*spinosus*				2			
Brown shrimp	*Argis*	*dentata*	3	3	3	3			
	Pasiphea	*tarda*					2		
	Pasiphea	*multidentata*				1			
Unidentified	*Pasiphea*					2			
	Sclerocrangon	*boreas*	3	3	2	2	2	2	
	Sclerocrangon	*ferox*				2			
Unidentified	*Sclerocrangon*					2			
	Spirontocaris	*gaimardi*			2				
	Spirontocaris	*phippsi*				2			
	Spirontocaris	*spinus*	2			1	2		
Unidentified	*Spirontocaris*			2	2	2			
	Eualus	*gaimardi*				2			
	Eualus	*belcheri*				2			
	Eualus	*fabricii*				2			
Unidentified	*Eualus*					2			
	Sabinea	*septemcarinata*	3	2					
Unidentified	*Sabinea*				2				
	Crangon	*septemspinosus*	1	1					

			Frequency class in regions						
Common Name	Family/Genus	Species	WHS	CHS	EHS	UB	RI	0B + 2G	Gr.
Fish									
Hagfish	*Myxine*	*glutinosa*						1	E
Greenland shark	*Somniosus*	*microcephalus*			2				E
Thorny skate	*Raja*	*radiata*	3	*2	3	3	*3	3	A
Spinytail skate	*Raja*	*spinicauda*				1	1		E
Jensen's skate	*Raja*	*jenseni*			1	1			E
Unidentified	Rajidae				2	2			
Unidentified	Chimaeridae						1		E
Capelin	*Mallotus*	*villosus*	2	2	2		2		D
Viperfish	*Chauliodus*	*sloani*					1		E
Krøyer's lanternfish	*Notoscopelus*	*krøyerii*						2	E
Largescale lanternfish	*Symbolophorus*	*veranyi*				1			E
Unidentified	Myctophidae				3	3	3	3	
Daggertooth	*Anotopterus*	*pharao*					1		E
Arctic cod	*Boreogadus*	*saida*	3	*3	2	3	*2	3	A
Atlantic cod	*Gadus*	*morhua*		1	1	1	1	2	E
Threebeard rockling	*Gaidropsarus*	*ensis*			2	3	*2	3	B
Longfin hake	*Urophycis*	*chesteri*				1			E
Roughhead grenadier	*Macrourus*	*berglax*				3	3	3	B

TABLE 2. (*continued*)

Common Name	Family/Genus	Species	Frequency class in regions						
			WHS	CHS	EHS	UB	RI	0B+2G	Gr.
Northern wolffish	*Anarhichas*	*denticulatus*				2			D
Atlantic wolffish	*Anarhichas*	*lupus*					1	2	E
Spotted wolffish	*Anarhichas*	*minor*				1	2	1	D
Unidentified	Anarhichadidae				2	2	2	2	
Stout eelblenny	*Anisarchus*	*medius*				2	2		D
Fourline snakeblenny	*Eumesogrammus*	*praecisus*		*1		1			E
Daubed shanny	*Leptoclinus*	*maculatus*					*2		E
Snake blenny	*Lumpenus*	*lumpretaeformis*			2		2		E
Unidentified	Stichaeidae				3	2	2	2	
Fish doctor	*Gymnelus*	*viridis*				1			E
Checkered wolf eel	*Lycenchelys*	*koethoffi*					*1		E
Common wolf eel	*Lycenchelys*	*paxillus*				2	1		D
Wolf eelpout	*Lycenchelys*	*verrilli*				2	2		D
Esmark's eelpout	*Lycodes*	*esmarki*		*2	2	2	2	3	B
Laval's eelpout	*Lycodes*	*lavalaei*				1			E
	Lycodes	*mucosus*	1	*1					E
Pale eelpout	*Lycodes*	*pallidus*	*2			1			E
Arctic eelpout	*Lycodes*	*reticulatus*	*2	*3	2	2	*2	2	A
Polar eelout	*Lycodes*	*polaris*				1			E
Vahl's eelpout	*Lycodes*	*vahlii*			2	2	2	3	B
Unidentified	Zoarcidae		3	3	3	3	3	2	
Redfish	*Sebastes*	spp.		*1	3	3	*3	2	B
Arctic hookear sculpin	*Artediellus*	*uncinatus*			2	3	*2	2	B
Polar sculpin	*Cottunculus*	*microps*				2	*1	1	D
Arctic staghorn sculpin	*Gymnocanthus*	*tricuspis*				1			E
Twohorn sculpin	*Icelus*	*bicornis*				2			D
Spatulate sculpin	*Icelus*	*spatula*		*1	2	2	*2		D
Grubby	*Myoxocephalus*	*aenaeus*			2	1	1		E
Longhorn sculpin	*Myoxocephalus*	*octodecemspinosus*			2				E
Shorthorn sculpin	*Myoxocephalus*	*scorpius*			2		2		E
Nybelin's sculpin	*Triglops*	*nybelini*	3	*3	3	3	*3	3	A
Mailed sculpin	*Triglops*	*murrayi*	1		3	3	*3	3	B
Ribbed sculpin	*Triglops*	*pingeli*	3	*3	3		*3		A
Unidentified	Cottidae		3	3	3	2	3	2	
Atlantic sea poacher	*Agonus(Leptagonus)*	*decagonus*	3	*3	2	2	*2	2	A
Atlantic alligatorfish	*Aspidophoroides*	*monopterygius*			2	2	2	2	B
Arctic alligatorfish	*Aspidophoroides*	*olriki*	2	*3	3	3	2	3	A
Lumpfish	*Cyclopterus*	*lumpus*			2	2	2	2	B
Leatherfin lumpsucker	*Eumicrotremus*	*derjugini*	2	*3		2	1		C
Spiny lumpsucker	*Eumicrotremus*	*spinosus*	3	*3	3	3	3	2	A
Longfin seasnail	*Careproctus*	*longipinnis*					2		E
Sea tadpole	*Careproctus*	*reinhardti*		*2	1	2	2		D
Atlantic seasnail	*Liparis*	*atlanticus*				2			D
Greenland seasnail	*Liparis*	*tunicatus*	*3	3		2	1	1	C
Polkadot seasnail	*Liparis*	*cyclostigma(gibbus)*	2	*3		2	*1		C
Gelatinous seasnail	*Liparis*	*koefoedi(fabricii)*	3	*3	3	3	*3	3	A
Unidentified	Cyclopteridae		3	3	3	3	3	3	
American plaice	*Hippoglossoides*	*platessoides*			2	2	2	2	B
Greenland halibut	*Reinhardtius*	*hippoglossoides*	3	*3	3	3	*3	2	A

B, C, and D were more frequent in the eastern, western, or central part of the study area, respectively. The remaining group (E, 25 species) comprised species found in only one region or too rare to establish a geographic pattern.

The first group (A) comprised 10 species occurring commonly (present in >10% of sets) in all regions (Table 2), among which were the thorny skate, Arctic cod, and Greenland halibut (also called turbot). The second group (B, 10 species) comprised species which were most frequent in the regions 0B + 2G and eastern Hudson Strait, often disappearing towards the central and western part of the strait. Representative species of this groups were the redfish, Atlantic lumpfish, roughhead grenadier, threebeard rockling, and American plaice. Clusters A and B were joined together at the 0.5 similarity level.

Group C comprised three species that are discontinuous but present at each end of the study area, with predominance in the west: the leatherfin lumpsucker, the Greenland and the polkadot seasnails. This discontinuous distribution could be due to insufficient sampling in eastern Hudson Strait proper (Table 1). Group D encompassed 11 species that occur less frequently (in

TABLE 3. Summary of the number of fish and decapod groups of each frequency class for each region. Frequency classes and regions are the same as in Tables 1 and 2.

	Frequency class	Region					
		WHS	CHS	EHS	UB	RI	0B+2G
Decapods	1	1	2	0	2	0	0
	2	2	2	7	14	5	6
	3	4	3	1	2	3	1
	Total	7	7	8	18	8	7
Fish	1	2	5	3	13	12	4
	2	6	4	19	23	23	16
	3	12	15	14	15	13	12
	Total	20	24	36	51	48	32

less than 10% of the sets) than groups A–C. Group D is most abundant in Ungava Bay and/or Resolution Island. Representative species are the stout eelblenny, the common wolf eel, the spatulate and two-horn sculpins. The importance of this group may be an artifact of the large sampling effort in these two regions. Finally, group E represented rare species such as the Greenland shark, the Atlantic cod, the shorthorn sculpin, and the longtail seasnail. Groups C and D merged at the 0.5 similarity level and clustered to group E at the 0.55 level before agglomerating (0.75) with the larger cluster formed by groups A and B.

Abundance of Common Species

Quantitative comparison of average catch rates (kg·0.5-h tow^{-1}) of common types of organisms (Table 4) characterizes each region and determines the inter-regional affinities. In western and central Hudson Strait, the average catch comprised Arctic cod, liparids, and spiny lumpsuckers, in decreasing order of abundance. The eastern part of the strait appeared as a transition zone in community composition, where pandalid shrimp and myctophids are not abundant, but turbot catches exceed those of western and central Hudson Strait. In Ungava Bay and off Resolution Island, catch composition was dominated by the striped pink shrimp, although the associated fish species differed between the two regions. Turbot, Arctic cod, and grenadiers were found in Ungava Bay, whereas low abundances of turbot, spiny skate, and lanternfish characterized catches off Resolution Island. In the Labrador Sea–Davis Strait areas, striped pink shrimp was replaced by pink shrimp (11.28 kg·tow^{-1}) as the most abundant pandalid. Fish species in 0B and 2G included Arctic cod, roughhead grenadier, and spiny skate. For all areas, average fish catch was low (< 50 kg·0.5-h tow^{-1}) and, if the massive catches of pandalid shrimps were excluded from the total, were highest in Ungava Bay and eastern Hudson Strait. In decreasing ranks, the abundance of pandalid shrimps, turbot, liparids, and Arctic cod exhibited the highest variance in average catch rate among regions.

Spatial vs. Temporal Variability in Catch Composition

The biogeographical analysis of all sets clustered with a spatial constraint (Fig. 3) showed the occurrence of three different types of clusters for both areas. First, numerous small clusters comprising one to three sets made by a single ship could be seen in the southeast and northeast areas of Resolution Island (Fig. 3a) and of Ungava Bay (Fig. 3b), respectively. For both

TABLE 4. Average catch rate of common decapods and fish by-catch species. Common species are given a frequency of 3 in Table 2, corresponding to an occurrence of at least 10% of sets in each region. (+), frequency 2 and 1, species present in fewer than 10% of the sets. (−) not recorded in the region. Regions are identified as in Table 1.

Species	Average catch rate (kg·0.5-h tow^{-1})					
	WHS	CHS	EHS	UB	RI	0B+2G
Decapods						
Pandalus borealis	+	+	2.06	0.9	0.32	11.28
Pandalus montagui	0.07	0.03	24.01	364.24	1271.08	+
Lebbeus spp.	+	+	+	0.51	−	−
Argis dentata	0.30	0.91	+	1.40	−	−
Sclerocrangon spp.	0.11	0.41	+	0.43	−	+
Fish and others						
Raja radiata	0.50	+	0.67	0.89	2.97	0.55
Myctophidae	−	−	2.40	0.02	0.93	0.49
Boreogadus saida	12.89	4.52	+	4.95	+	1.23
Gaidropsarus ensis	−	−	+	0.49	+	0.22
Macrourus berglax	−	−	−	3.79	0.20	3.17
Zoarcidae	1.36	0.33	0.77	0.57	0.01	+
Sebastes spp.	−	+	0.31	0.86	0.28	+
Artediellus uncinatus	−	−	0.28	0.16	+	+
Triglops spp.	1.41	0.45	0.23	0.14	0.67	+
Aspidophoroides spp.	0.03	0.02	0.19	0.07	0.07	0.13
Cyclopterus lumpus	−	−	+	+	+	0.28
Eumicrotremus spinosus	1.93	1.30	0.73	0.39	0.57	+
Liparidae	9.67	5.62	1.62	2.52	0.32	0.23
Reinhardtius hippoglossoides	0.35	0.63	7.12	15.32	1.03	+
Gonatus sp.	+	+	0.01	0.02	0.01	0.05
Total	28.62	14.22	40.40	396.86	1278.53	17.63

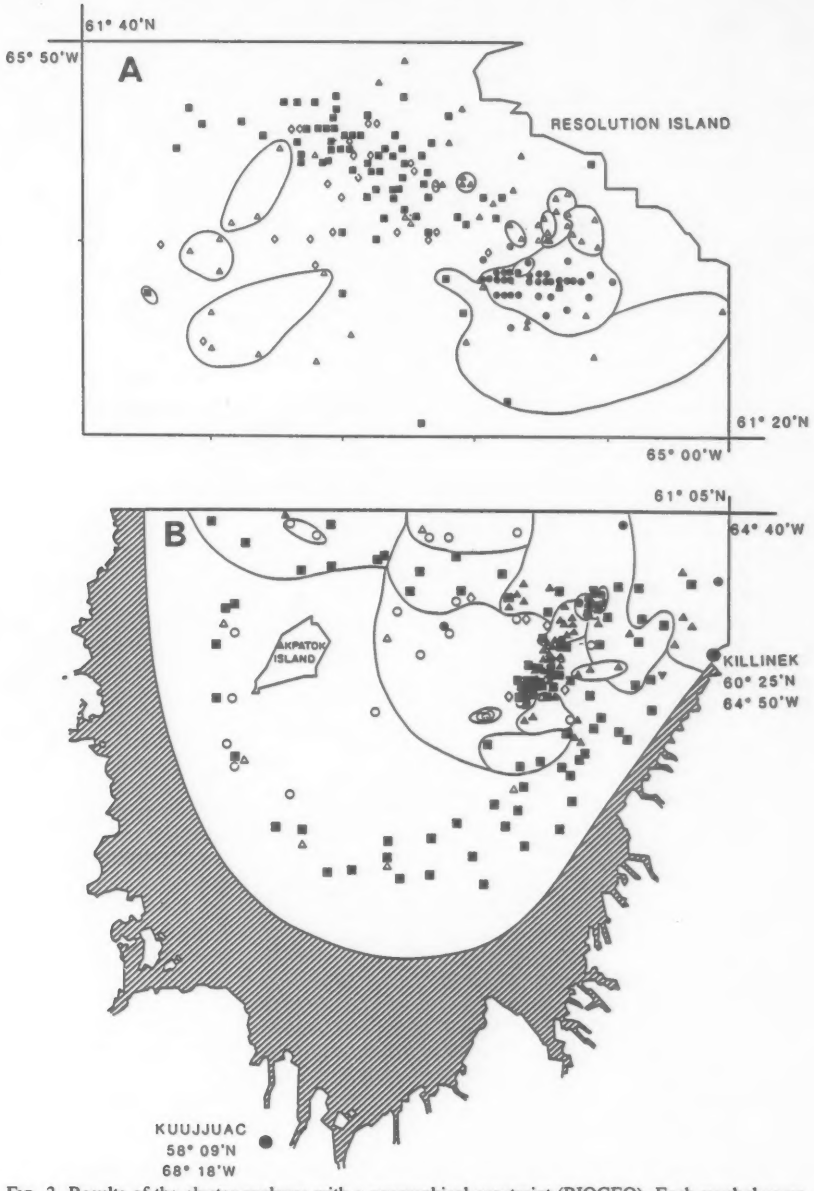

FIG. 3. Results of the cluster analyses with a geographical constraint (BIOGEO). Each symbol represents a standard set carried out by a different ship. Zones circled by a continuous line indicate groups of sets exhibiting a homogeneous species composition and abundance.
A. Resolution Island
B. Ungava Bay.

areas, these sets were located in deep water (> 300 m), where high shrimp catches were made. Both areas had similar T-S characteristics (Fig. 2). It is possible that the very large number of sets made in those areas could have artificially increased the number of clusters, although their density also corresponds to the high year-to-year variability in shrimp catches in both areas.

Second, clusters of five to 20 sets, covering a larger surface area than the previous types, could be observed along the outer edge of the bank. Those medium-sized clusters comprised the catches of two or more ships, indicating a more stable catch composition from year to year than the previous type. Five clusters were identified along the northern edge of the bay, distinguishing catches made on the Ungava Bay shelf (< 300 m) from those made at the edge of Hudson Strait (> 300 m).

Third, the remainder of the sets located on the inside part of the bank clustered in a single large group, indicating the occur-

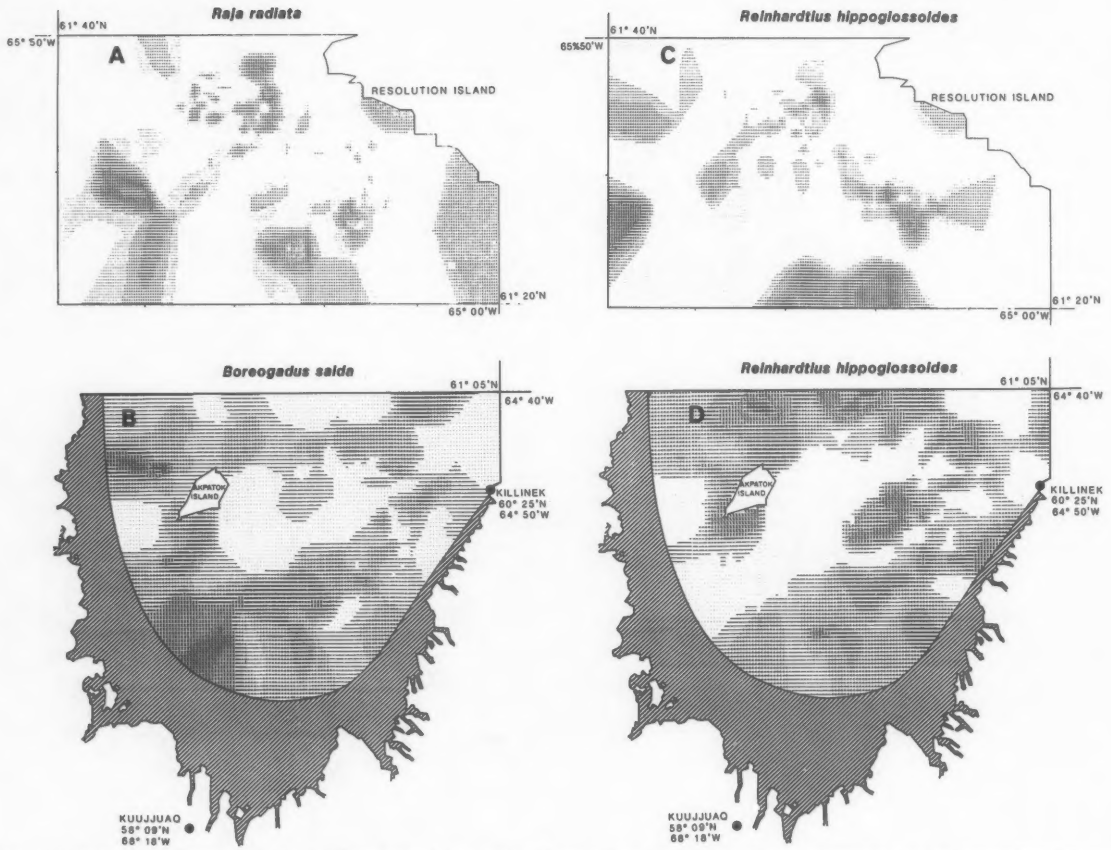

FIG. 4. Distribution of decapod species off Resolution Island and in Ungava Bay. Each shade of grey represents an abundance class expressed as the naperian logarithm ($\ln(x + 1)$) of the total weight (kg) caught during a standard 0.5-h tow.
A. *Pandalus montagui* off Resolution Island.
B. *Pandalus montagui* in Ungava Bay.
C. *Pandalus borealis* off Resolution Island.
D. *Argis dentata* in Ungava Bay.

rence of large areas of homogeneous species composition. This pattern differed from the previous ones as it resulted from the catches of several ships over different years therefore obviating major differences in ships' performance. The occurrence of a variety of cluster types and locations off Resolution Island and in Ungava Bay indicates that spatial variability is related to environmental conditions.

The shape and distribution of the biogeographical clusters (homogeneous zones) indicated a link with water circulation pattern as well as depth in Ungava Bay. The medium-sized clusters at the edge of the bank also corresponded with the location of highly mixed transition zones (Drinkwater and Jones 1987), whereas the large cluster in central Ungava Bay reflected the cyclonic circulation of Arctic waters into the bay (Fig.2).

Mapping of Regional Decapod Distribution

The striped pink shrimp (*P. montagui*) occurs throughout the Resolution Island area, with a high concentration at the southeast edge of the bank (Fig. 4a). This map groups data from all research cruises; it shows the general pattern of this species abundance without allowing for the year-to-year variability previously documented using biogeographic clustering. Diel vertical migrations of shrimps also affected the catch at any given location depending on the time of sampling (Fréchette et al. 1984; C. Hudon, unpubl. data) and further contributed to the abrupt transition between extremely high and low shrimp concentrations.

In Ungava Bay, the striped pink shrimp was present mostly in the northeastern part, but also exhibited highly variable concentrations within this area (Fig. 4b). Concentrations appeared along an axis parallel to the coastline, in a fashion similar to Resolution Island, roughly corresponding to the northern part of a channel deeper than 300 m (Fig. 1). For all tows made in Ungava Bay, striped pink shrimp was the most common shrimp encountered. This species was also occasionally abundant in eastern Hudson Strait (NE of Cape Hope Advance) (50–100 $kg \cdot tow^{-1}$: MacLaren Marex Ltd. 1978; Allard 1980).

Pink shrimp (*P. borealis*) was concentrated in the deepest areas at the southern edge of the Resolution Island bank (Fig. 4c), as well as in the northern part of Ungava Bay. Its abundance remained low in comparison with striped pink shrimp (up to 20 $kg \cdot tow^{-1}$) and was restricted to the deep central trench in eastern Hudson Strait. In 0B + 2G, until the 1988–

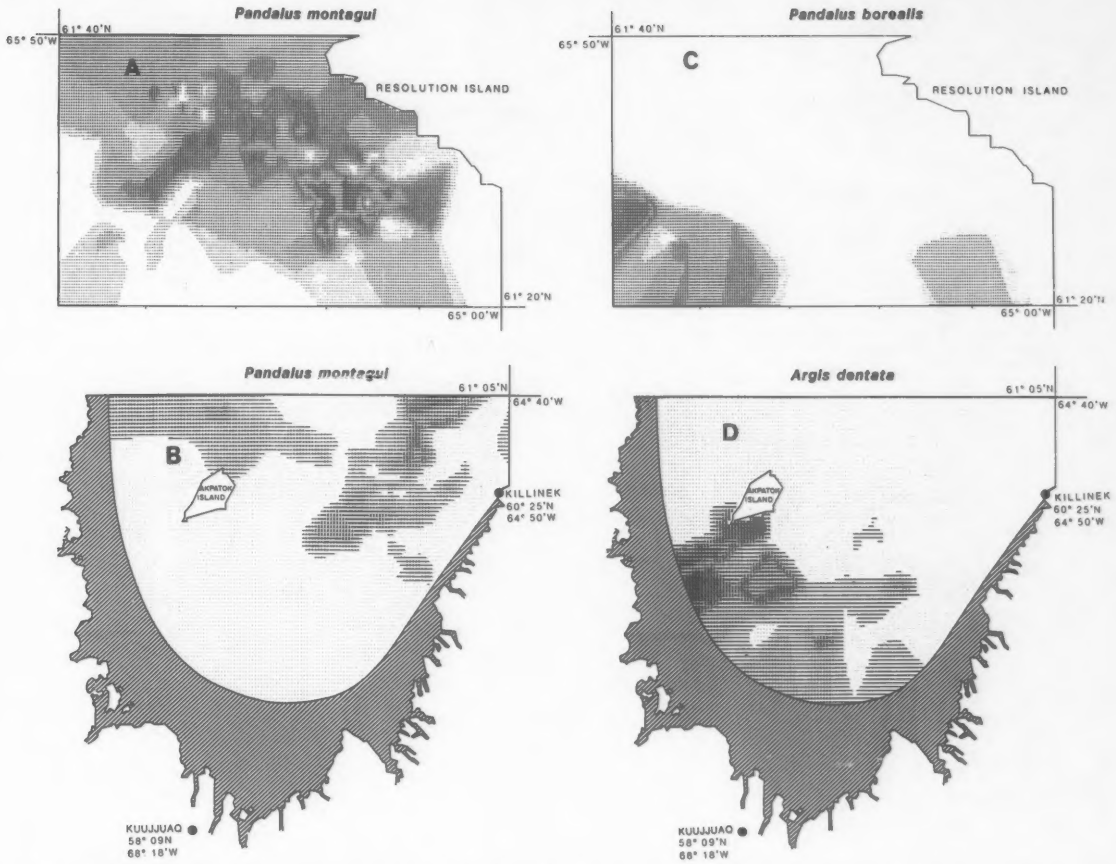

FIG. 5. Distribution of fish by-catch species off Resolution Island and in Ungava Bay. Each shade of grey represents an abundance class expressed as the naperian logarithm ($\ln(x + 1)$) of the total weight (kg) caught during a standard 0.5-h tow.
A. *Raja radiata* off Resolution Island.
B. *Boreogadus saida* in Ungava Bay.
C. *Reinhardtius hippoglossoides* off Resolution Island.
D. *Reinhardtius hippoglossoides* in Ungava Bay.

89 fishing season, only low concentrations were found in small sectors off Cumberland Sound (Div. 0B) and along the northern Labrador coast (Div. 2G), increasing towards Divisions 2JH to the south and Divisions 0A, 1A, and 1B to the north (NAFO 1987).

The brown shrimp, *Argis dentata*, was abundant only in southwestern Ungava Bay (Fig. 4d), in the area of Arctic waters. It has been reported mostly in waters <0°C between 50 and 200 m (Squires 1966). This species was recorded as having the second largest catch in Ungava Bay, with a total weight of 208.6 kg (Allard 1980). Its apparent abundance in Ungava shelf waters makes it a possible target for local exploitation.

Mapping of Regional Fish Distribution

Thorny skate were found over the entire area near Resolution Island with a patchy distribution, without a particular pattern (Fig. 5a). On the Scotian Shelf, this species inhabits a wide range of depth (30 to >400 m), temperature (0–13°C) and salinity (31–34 $mg \cdot L^{-1}$), although it is most concentrated in cool (2–5°C) and shallow (40–100 m) water (Scott 1982). The tolerance of thorny skate with respect to environmental conditions is demonstrated by its occurrence in the Labrador Sea (Backus 1957), Hudson Strait, and in Hudson Bay (Vladykov 1933).

Arctic cod was not abundant off Resolution Island, but occurred everywhere in Ungava Bay. It exhibited a circular pattern of density from the highest in the south and west of the bay, progressively decreasing to a near absence in the center of the bay (Fig. 5b). This distribution pattern was similar to that of the seasnails. Sizes ranged from 7.4 to 24.6 cm, with many between 10–16 cm. Arctic cod is pelagic, from the surface to 800 m (Leim and Scott 1966), and its occurrence in a shrimp trawl is not representative of its real abundance. Previous collections of Arctic cod in the Labrador Sea were made at temperatures ranging from −1.85°C to 2.52°C, although in only one instance was the temperature above −1.0°C (Backus 1957).

Greenland halibut exhibited a patchy abundance along the edge of the Resolution Island bank, extending towards the

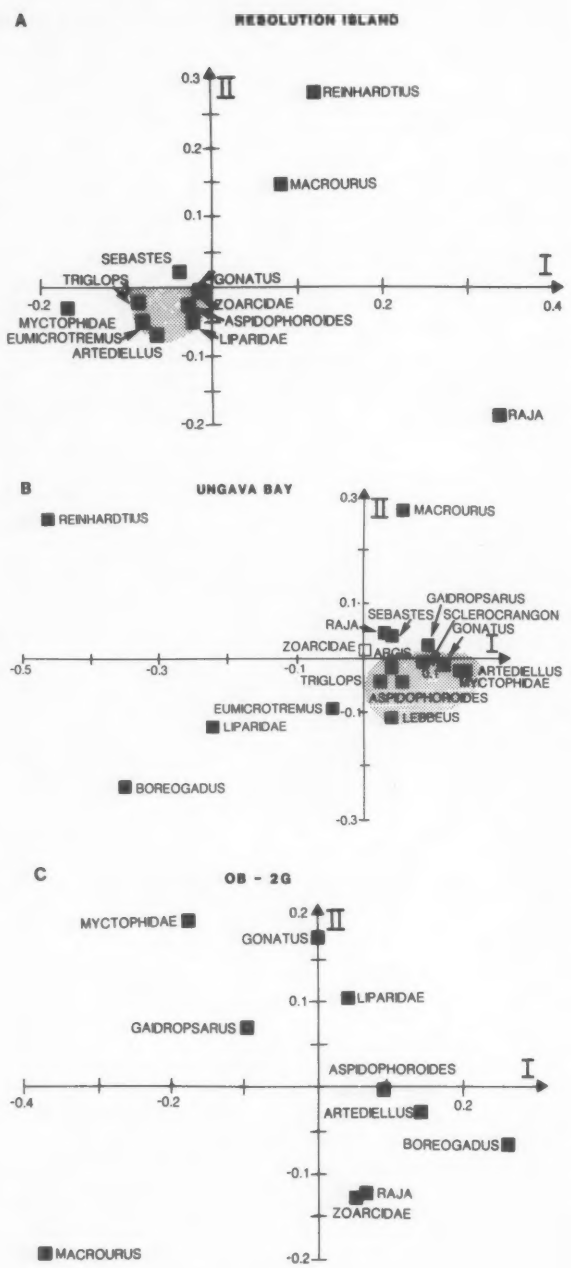

FIG. 6. Principal coordinate analyses of fish by-catch abundance (ln(x + 1) transformed), allowing comparison of the relative positioning of associated species in the reduced, two-axes space. Species located in the same quadrat, or in the neighbourhood of each other relative to others are associated. Pandalid shrimp were excluded from the analysis since their single variability in abundance masked that of fish by-catch.
A. Resolution Island.
B. Ungava Bay.
C. 0B + 2G.

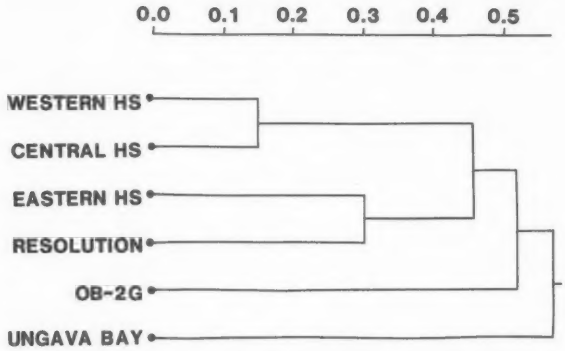

FIG. 7. Cluster analysis of the species abundance (ln(x + 1)) for the six regions of the study area, showing the biogeographic affinities with respect to common species abundance.

northwest (Fig. 5c). Similarly, in Ungava Bay, its highest concentrations were located along the eastern edge of Akpatok bank and across the mouth of the bay, in water >400 m (Fig. 5d). This species is abundant in deep water (200–600 m or more) (Bigelow and Welsh 1924; Scott 1982), usually at temperatures of −0.5°C to 3°C (Templeman 1973). Turbot was commonly found throughout the study area to western Hudson Strait, but was not captured west of 79°00W (northern Hudson Bay, Foxe Channel, 26 sets).

Redfish were concentrated at the southeastern edge of Resolution Island, in the deeper areas (>200 m) influenced by Labrador Sea waters. A similar distribution was found in northern Ungava Bay, where redfish occurred sporadically, concentrated in the deep waters (Jarry 1988). Most individuals were smaller than 10 cm. Redfish inhabit a wide range of temperature, and although it has been described as an Arctic species (which is true in the sense that its range extends into the Arctic Seas), it is confined to deep (100–600 m), relatively warm (>1.7°C) waters of Atlantic origin and avoids the layers of cold Arctic waters in Davis Strait, Labrador Sea, as well as in the Gulf of St. Lawrence (Bigelow and Welsh 1924; Leim and Scott 1966; May 1969).

Fish Species Assemblages

A more detailed look at species associations within regions can be obtained using the projection of the fish species on the first two axes of the principal coordinates. For each region, species belonging to the same quadrat and exhibiting high values of the projection were examined (Fig. 6) in relation with species occurring in opposing quadrats. The first group consisted of small, noncommercial species such as *Triglops* spp., *Aspidophoroides* spp., *Eumicrotremus* spp., and Myctophids, which formed a low-variability, background assemblage in Resolution Island (Fig.6a) and Ungava Bay regions (Fig.6b). Another more distinct Arctic association was that of *Boreogadus* and Liparidae, located in the same (Ungava Bay, Fig. 6b) or adjacent (0B + 2G, Fig. 6c) quadrats.

In 0B + 2G, Axis II separated the previously described Arctic from the Labrador Sea (Myctophidae, *Gaidropsarus*, and *Macrourus*) assemblages. For the three regions, *Macrourus* and *Reinhardtius* exhibited a loose association, being either in the same or in adjacent quadrats. *Reinhardtius* appeared more closely associated to the Labrador Sea component than with the arctic assemblage, as it was located in the quadrat opposite to

the arctic assemblage in Ungava Bay and Resolution Island. This indicates a negative co-variation in abundance between these two groups.

Depending on the area, *Raja* exhibited a strong variability on its own (Fig.6a), an intermediate variability with an arctic group (Zoarcidae, Fig. 6c), or a low variability with Labrador Sea components (*Sebastes, Gaidropsarus,* Fig. 6b). This observation reflects the adaptability of the thorny skate to a variety of environmental conditions in the north Atlantic (Scott 1982). To summarize, the analysis indicates the occurrence of two basic fish associations, showing the predominance of western (Arctic) or eastern (Labrador Sea) fauna, which broadly overlap in the study area. The Arctic association dominate in Resolution Island and Ungava Bay, while the Labrador Sea association is more important in 0B + 2G.

Large Scale Geographic Zonation

The cluster analysis on the regional abundance of common species of fish and invertebrates shows that Hudson Strait is a continuum along the west to east gradient (Fig. 7). The common species and their abundance levels are most similar in the western and central areas. These two areas have a less diverse fauna and a lower biomass than the more easterly regions. Western and central regions do not have any exclusive species: they comprise species that are found commonly elsewhere.

The second regional group is composed of eastern Hudson Strait and Resolution Island. This is to be expected since Resolution Island was somewhat artificially distinguished from the rest of the eastern strait on the basis of its high pandalid shrimp catches. However, the remainder of the fish and decapod fauna is sufficiently similar, both in terms of species frequency as well as abundance, to warrant their early clustering.

The east–west continuum of Hudson Strait is demonstrated by the subsequent clustering of the four above regions, followed by the integration of the region 0B + 2G. It is only after the formation of that large group that Ungava Bay eventually joins it. The late clustering of Ungava Bay to the rest of the study area emphasizes the very distinct, diverse nature of its faunal composition and abundance in comparison with the other regions.

Discussion

Comparisons among several ships must be made with caution due to the differences in performances of vessels, gears, and crews, which are indistinguishable from year-to-year variations in catchable biomass. For exploratory/cost-recovery cruises without a predetermined randomized sampling plan, sets converged and clustered in areas of high shrimp concentration. The lack of an accurate positioning system in Hudson Strait and Ungava Bay caused imprecisions in location and area covered by each tow. Also, the absence of accurate depth charts contributed to gear damage and resulted in inadequate depth stratification of fishing grounds. The fish species sampled in this study reflect the fishing gear used and correspond to those associated with shrimp, which was the principal target species. Such sampling has its limitations, since characteristic coastal Arctic species such as Greenland cod (*Gadus ogac*) and four-horned sculpin (*Myoxocephalus quadricornis*) were not reported in the samples. Also, pelagic species such as Arctic cod, myctophids, and Greenland shark cannot be adequately sampled with deep-water bottom trawling. However, once the above factors are accounted for, the information on decapod and fish assemblages provides a valid basis for large scale geographic comparisons.

The segregation of two pandalid species over the study area is consistent with previous studies of their temperature tolerance. *Pandalus montagui* tolerates a wider range of temperature (−1–20°C) (Allen 1963; Squires 1968) and of depth than *P. borealis* (0–11°C) (Simpson et al. 1970; Fontaine 1970). Of all the pandalids in the northwest Atlantic, *P. montagui* is the only one which inhabits colder Arctic waters (Squires 1957, 1966). The dominance of *P. borealis* in the Davis Strait–Labrador Sea area to 75°N (Squires 1966) therefore appears related to the extent of the influence of Atlantic waters, maintaining bottom water temperatures above 1°C (Schroeder 1963) independent of latitude. Central Ungava Bay, western, and central Hudson Strait supported consistent catch of other arctic decapod species (*Lebbeus* spp., *Argis dentata, Sclerocrangon* spp.), showing their Arctic dominated waters.

There have been few attempts to formally define the nature and characteristics of "Arctic" fish species (Dunbar and Hildebrand 1952; McAllister 1975). Generally, that definition includes species with their center of distribution in the Arctic and exhibiting tolerance to low temperatures (Bigelow and Welsh 1924; Backus 1957; Morin and Dodson 1986). Arctic species listed in McAllister et al. (1975) comprise all fish species found in the Arctic, even though some of them belong to temperate regions (e.g. brook trout).

Cottids (McAllister 1960), and other species of non specialist benthic feeders (McAllister 1975) are the best represented fish groups in the Arctic. The low number of total and endemic fish species in the Arctic was attributed to the low temperature and low productivity, lack of food resources, and ice action in the littoral zone (McAllister 1960; McAllister et al. 1975). In this study, Ungava Bay and Resolution Island supported roughly twice as many species of Zoarcidae, Cottidae, and Cyclopteridae as reported in the waters adjacent to northern Labrador Sea–Davis Strait. Of all regions, Ungava Bay supported the highest diversity and abundance of fish and decapod species. Its fauna comprised elements of 0B–2G and of the Hudson Strait regions. Such species overlap from adjacent regions is in part made possible by the simultaneous Arctic and Labrador Sea influences. However, other regions (Resolution Island and eastern Hudson Strait) under such influence do not exhibit a comparable richness. In Ungava Bay, a variety of bottom types are likely to occur in shallow bank, sloping shelf, and deep trench areas. In addition, it is likely that the intense tidal mixing with local freshwater result in increased nutrients and warmer temperatures, and thus could enhance local primary production relative to other regions of Hudson Strait.

With respect to biological production, it is noteworthy that Resolution Island and northeastern Ungava Bay, where high striped, pink shrimp concentrations are found, exhibited common hydrographic features. Both areas are subjected to strong tidal currents (Canadian Hydrographic Service 1987), and are located in the transition zone between heavily mixed and stratified waters (Drinkwater and Jones 1987). This likely explains the high level of temporal variability in the biogeographical analysis of catches found off Resolution Island and in the northeastern area of Ungava Bay. Areas of extensive water mixing combined with high planktonic primary productivity, located along the southern edge of Baffin Island (Drinkwater and Jones 1987) could possibly generate high levels of secondary production off Resolution Island. The high standing stock of striped

pink shrimp in eastern Hudson Strait could thus be related to the high copepod biomass on which it primarily feeds (C. Hudon, unpubl. data).

Oceanographic zonation can be mapped and defined on the basis of combined physical characteristics of temperature–salinity relationships and biogeographical data (Dunbar 1951; Dunbar and Hildebrand 1952). Three zones can be defined in our study area, corresponding to the major groups of fish species observed in the principal coordinates analysis. First, an Arctic zone, in which water temperature equals or is below 0°C and salinities are 31–34 ‰ (Fig. 2). These waters were found in western and central Hudson Strait and southern Ungava Bay. These areas have a low species richness and are characterized by a scattered biomass of non-commercially exploitable species such as Arctic cod (*Boregadus saida*) and liparids.

At the other end of the continuum is the subarctic zone, under the simultaneous influence of the cold Baffin Island Current and the warmer West Greenland and Labrador Currents, where temperatures are between −1 and 4.0°C and salinities are 32–34.5 ppm (Fig. 2; Dunbar 1951). Fish inhabiting these waters endure a considerable Arctic influence, although not tolerating the very cold water of pure Arctic origin (Backus 1957). This group is represented by the Greenland halibut, grenadiers, three beard rockling and, occasionally, by the thorny skate (Fig. 6; see Dunbar and Hildebrand 1952 for additional species). In divisions 0B–2G, these species were the foremost demersal species captured, accounting for more than 95% of the total catches in those areas (NAFO 1987).

The transition zone between Arctic and subarctic waters begins at the mouth of Hudson Strait and extends over Ungava Bay and eastern Hudson Strait in a SE—NW wedge. Its most remarkable feature is the change of dominance from *Pandalus borealis* to *P. montagui*, attributable to the greater influence of Arctic waters west of the entrance. However, a small population of *P. borealis*, either indigenous or carried by water movements, occurs in the deep portion of the strait where deep Labrador Sea water penetrates (Fig. 2). Water circulation exerts a strong influence on shrimp distribution in eastern Hudson Strait, explaining the high year-to-year variability in catches off Resolution Island and northeastern Ungava Bay (Fig. 3). Furthermore, the occasional high catches of *P. montagui* observed outside of the areas of concentrations (NE of Cape Hope Advance and across the mouth of Ungava Bay) (Fig. 4b) could result from advective losses from the Resolution Island area into the gyre located north of Ungava Bay (Fig. 1). The influence of circulation on pandalid shrimp stock identity in eastern Hudson Strait should be further studied.

Year-to-year variation is also perceptible in pink shrimp catches in the Labrador Sea–Davis Strait areas. Until 1988, total catches in neighbouring Divisions 0A, 1CDE, and 2JH, located north, east, and south, respectively, constantly exceeded those in 0B–2G by one to two orders of magnitude. This difference has been attenuated by a recent increase in shrimp catches in the 0B–2G Divisons in 1988 and 1989.

Large scale environmental phenomena, such as climatic or hydrographic changes, could exert influence over the location and abruptness of the transition zone, possibly explaining spatial and temporal variability of shrimp catches. One example is the effect of ice distribution along the west Greenland coast on Atlantic cod abundance (Jensen 1948; Vibe 1967). Off the coast of northern Labrador, a similar phenomenon could at least partially explain the variability in the abundance of capelin (Dunbar 1975) and Atlantic cod (Gillis and Allard 1986). The fluctuations of pandalid catches in this highly dynamic transition zone could offer some potential to monitor long term climatic changes affecting eastern Canadian Arctic waters.

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Territory Size as a Predictor of the Upper Limit to Population Density of Juvenile Salmonids in Streams

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We examined the old, but untested hypothesis that territory size limits the maximum population density of salmonids in streams. We used published data to derive an interspecific regression of territory size (m^2) on fork length (cm) ($\log_{10}$ territory size = 2.61 $\log_{10}$ length — 2.83, $r^2 = 0.87$, $n = 23$). Growth and mortality trajectories of salmonid cohorts from eight experimental studies were compared to the maximum-density regression, the inverse of the territory–size regression. In shallow habitats, such as riffles and raceways, the cohort trajectories followed the maximum density regression quite closely and were consistent with the territory–size hypothesis. In addition, natural densities in eight other studies did not exceed the predicted maximum density and tended to fall within the 95% C.L. of the maximum-density regression. Data from shallow habitats, therefore, provide strong support for the territory–size hypothesis. A linear logistic response model showed that the probability of observing density-dependent growth, mortality, or emigration increased significantly with increasing values of an index of habitat saturation, developed from the territory–size regression. Our results suggest that the territory–size regression has practical value for predicting the maximum densities of stream-dwelling salmonids in shallow habitats and the occurrence of density-dependent population responses.

Nous avons étudié l'ancienne hypothèse non vérifiée selon laquelle la superficie du territoire limite la densité maximale de population des salmonidés dans les cours d'eau. Nous avons utilisé les données existantes afin de dériver une régression interspécifique de la superficie du territoire (m^2) à la longueur à la fourche (cm) ($\log_{10}$ superficie du territoire = 2,61 $\log_{10}$ longueur — 2,83, $r^2 = 0,87$, $n = 23$). Les trajectoires de croissance et de mortalité de cohortes de salmonidés provenant de huit études expérimentales ont été comparées à la régression de densité maximale, l'inverse de la régression de la superficie du territoire. Dans le cas d'habitats en eau peu profonde avec courant rapide, les trajectoires des cohortes suivaient la régression de la densité maximale assez étroitement et elles étaient conformes à l'hypothèse de la superficie du territoire. De plus, les densités naturelles dans huit autres études ne dépassaient pas la densité maximale prévue et avaient tendance à se trouver dans l'intervalle de la limite du seuil de confiance de 95% de la régression de la densité maximale. Les données concernant les habitats en eau peu profonde appuient donc fortement l'hypothèse de la superficie du territoire. Un modèle de réponse logistique linéaire a montré que la probabilité d'observer une croissance, une mortalité ou une émigration dépendante de la densité augmentait significativement avec les valeurs croissantes d'un indice de saturation de l'habitat, élaboré à partir de la régression de la superficie du territoire. Il semble, d'après nos résultats, que la régression de la superficie du territoire a une valeur pratique pour prévoir la densité maximale des salmonidés dans les habitats avec cours d'eau peu profondes et l'occurence des réactions de la population dépendante de la densité.

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Juvenile salmonids in streams commonly defend feeding territories (Dill et al. 1981; McNicol et al. 1985; Puckett and Dill 1985). This territorial behaviour has been hypothesized to play a role in limiting population density (e.g. Chapman 1966; Allen 1969; Mortensen 1977; Elliott 1984a). If a minimum territory size exists, then territoriality will limit maximum population density because excess individuals that do not acquire a territory presumably die or emigrate. The best evidence that territoriality can limit the population density of animals comes from studies of breeding birds (for a review, see Patterson 1980; Gauthier and Smith 1987). Similar evidence for stream-dwelling salmonids is lacking, but flat-topped stock-recruitment curves (see Solomon 1985 for a review) are at least consistent with the hypothesis that territoriality limits population density.

There is not necessarily a logical link between territoriality and the limitation of population density. If territory size is inversely proportional to population density and there is no minimum territory size, then territoriality would play no role in limiting density. Behavioural ecological studies of stream-dwelling salmonids are more consistent with the view that territory size is flexible rather than rigid. Not all individuals defend territories (McNicol et al. 1985; Puckett and Dill 1985; Grant and Noakes 1988), and when they do, territory size is influenced by the abundance of food and intruder pressure (Slaney and Northcote 1974; Dill et al. 1981; McNicol and Noakes 1984). In addition, territoriality in animals often ceases at high population densities (see Wilson 1975, p. 296–297) when the costs exceed the benefits of defence. Juvenile salmonids may

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conform to this generalization because they appear to switch from territorial to schooling behaviour when population densities are sufficiently high (Kalleberg 1958; Kawanabe 1969).

Despite scepticism (e.g. Noakes and Grant 1986) about the hypothesis that territory size limits population density (hereafter, the territory–size hypothesis), the resolution of this question has important management implications, because the territory–size hypothesis predicts maximum population densities which should not be exceeded by stocking or escapement quotas. In a stimulating paper, Allen (1969) suggested a unique way to test the territory–size hypothesis. The inverse of a regression of territory size on body size (the maximum-density regression) predicts the maximum density of a salmonid population that is composed of a single size-class. Allen (1969) could not test the territory–size hypothesis rigorously because he lacked sufficient territory–size data. However, his data suggested that space was not limiting because only 2–20% of the habitat appeared to be occupied by territories. But, instead of rejecting the territory–size hypothesis, Allen concluded that only 2–20% of the habitat has the right environmental features for the territories of any single size-class of fish.

Many studies have investigated the effects of population density on growth, mortality, or emigration rate (e.g. Le Cren 1973; Egglishaw and Shackley 1977; Mortensen 1977; Elliott 1984a) or tested the general idea that space may limit salmonid population density (e.g. Chapman 1962; Mason 1969). However, no study has attempted to test quantitatively the hypothesis that territory size limits density. Therefore, our purpose was to reexamine this old question using a large database. We had three specific objectives: (1) to develop an interspecific regression of territory size vs. body size for juvenile stream-dwelling salmonids, (2) to test quantitatively the territory–size hypothesis by comparing population-density data from the literature with the maximum-density regression, and (3) to determine whether the maximum-density regression can predict the occurrence of density-dependent changes in growth, mortality, or emigration. Our study included data for seven species: coho salmon (*Oncorhynchus kisutch*), chinook salmon (*O. tshawytscha*), rainbow trout (*O. mykiss*, formerly *Salmo gairdneri*), cutthroat trout (*O. clarki* formerly *Salmo clarki*), Atlantic salmon (*Salmo salar*), brown trout (*S. trutta*), and brook trout (*Salvelinus fontinalis*).

Allometry of Territory Size

Methods

We searched the literature for data relating territory size to body size of stream-dwelling salmonids, starting with Dill (1978). We included only studies where territory size was measured directly and did not include those where territory size was inferred from the inverse of population density. Some authors did not explicitly say how territory size was measured, but most appeared to use a version of the minimum-convex-polygon method (Schoener 1981). When studies reported territory sizes for fish under different conditions, such as high or low intruder pressure or high or low food density, a datum was included for each environmental condition, rather than calculating an average territory size. Because errors in the estimate of body size are much less than in territory size, we used the least-squares method to regress territory size on body size.

The interspecific regression was compared to a regression for brook trout (Grant et al. 1989). The brook trout regression underestimated territory size because it was based on average territory radius rather than the convex-polygon method. As

TABLE 1. Territory sizes of stream-dwelling salmonids.

Number[a]	Species[b]	Conditions[c]	n[d]	Territory area (m^2)	Fork length (cm)	Source
1.	*S.s.*	F	3	0.970	10.0	Stradmeyer and Thorpe 1987
2.	*S.s*	F	3	1.633	13.0	Stradmeyer and Thorpe 1987
3.	*S.s.*	ST-high ration	8	1.136	11.4	Symons 1971
4.	*S.s.*	ST-low ration	9	1.120	11.8	Symons 1971
5.	*S.s.*	ST	—	0.011	2.5	Kalleberg 1958
6.	*S.s.*	ST	—	0.030	4.5	Kalleberg 1958
7.	*S.t.*	ST	1	4.0	23.0	Kalleberg 1958
8.	*O.m.*	A	2	0.043	4.3	Stringer and Hoar 1955
9.	*O.m.*	A	2	0.050	5.3	Stringer and Hoar 1955
10.	*O.m.*	A	2	0.118	6.3	Stringer and Hoar 1955
11.	*O.m.*	ST-low prey	4	0.037	2.5	Slaney and Northcote 1974
12.	*O.m.*	ST-intermediate prey	6	0.018	2.5	Slaney and Northcote 1974
13.	*O.m.*	ST-high prey	6	0.010	2.5	Slaney and Northcote 1974
14.	*O.m.*	A	7	0.258	7.6	Yamagishi 1962
15.	*O.k.*	A	2	0.066	4.3	Stringer and Hoar 1955
16.	*O.k.*	A	2	0.088	5.3	Stringer and Hoar 1955
17.	*O.k.*	A	2	0.113	6.3	Stringer and Hoar 1955
18.	*O.k.*	F-high intruder pressure	12	0.131	4.5	Dill et al. 1981
19.	*O.k.*	F-low intruder pressure	9	0.199	4.5	Dill et al. 1981
20.	*O.k.*	ST-riffles	—	0.195	6.5	Mason 1969
21.	*O.k.*	ST-pools	20	0.130	6.5	Mason 1969
22.	*S.f.*	ST	8	0.110	5.4	McNicol and Noakes 1981
23.	*S.f.*	F	6	0.340	4.6	McNicol et al. 1985

[a]Numbers refer to data in Fig. 1.
[b]*S.s.* = Atlantic salmon; *S.t.* = brown trout; *O.m.* = rainbow trout; *O.k.* = coho salmon; *S.f.* = brook trout.
[c]F = field, unconfined fish in a natural stream; ST = stream tank with directional water currents; A = aquarium with weak directional water currents.
[d]n = number of fish observed.

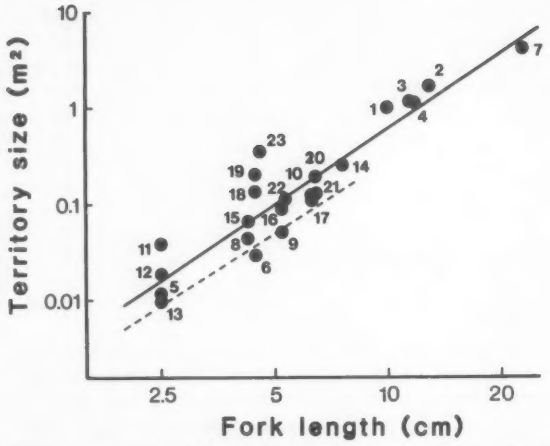

FIG. 1. Interspecific relationship between territory area (m^2) and fork length (cm) for stream-dwelling salmonids; numbers refer to data in Table 1. The equation of the least-squares regression is $\log_{10}$ area = 2.61 $\log_{10}$ length − 2.83, $r^2 = 0.87$, $n = 23$, $P<0.001$; 95% C.L. for the slope and intercept are 2.15–3.07 and −3.19 to −2.46, respectively. The dashed line is the territory-size regression for brook trout ($\log_{10}$ area = 2.48 $\log_{10}$ length − 2.84, $r^2 = 0.70$, $n = 23$, $P<0.001$; 95% C.L. for the slope is 1.74–3.22; data from Grant et al. 1989). The brook trout data were multiplied by 1.64 to make them comparable to the interspecific data. For the sake of graphical presentation, the uncorrected regression is shown (*y*-intercept = −3.05).

Grant et al. (1989) discuss, the latter method gave a result that was 1.64 times larger than the former, so territory sizes of brook trout were multiplied by 1.64 to correct for this bias.

To calculate a general mass (g) vs. fork length (cm) regression for stream-dwelling salmonids, we used regressions in Carlander (1969) supplemented with those in Brett and Glass (1973), Gee et al. (1978b), Englert et al. (1982), and Elliott (1985). A mean slope and intercept were calculated for each of sockeye salmon, rainbow trout, cutthroat trout, Atlantic salmon, brown trout, and brook trout. The overall regression was calculated as the mean for the six species: $\log_{10}$ mass = 3.03 $\log_{10}$ fork length − 1.93.

Results

We found territory-size data for five species in 10 different studies (Table 1). Territory size (m^2) increased with increasing body length (cm) (Fig. 1):

$$\log_{10} \text{area} = 2.61 \log_{10} \text{length} - 2.83.$$

Given the diverse environmental conditions under which the studies were conducted, body size explained a surprisingly high percentage of the variation in territory size. There were no obvious differences among species in territory size, but there was an order-of-magnitude variation about the line that appeared related to environmental conditions. For example, points 11, 12, and 13 reflect an inverse relation between food density and territory size (see Slaney and Northcote 1974), whereas points 18 and 19 reflect the inverse relation between intruder pressure and territory size (see Dill et al. 1981).

Also shown in Fig. 1 is the territory size — body size regression for young-of-the-year brook trout (Grant et al. 1989). No significant differences occurred between the slopes of the regressions (ANCOVA, $P = 0.80$), and the intercept of the corrected brook trout regression was almost identical to the intercept of the interspecific regression, and was well within its 95% C.L. (−3.17 to −2.46). The similarity of the two regressions gave us more confidence in the validity of the interspecific regression. We used the interspecific regression to test the territory–size hypothesis because it includes data for five of the seven species in our study.

Discussion

Territory size increased as a power function of body length raised to exponents between 2.48 and 2.61 (Fig. 1). Because body mass (M) increases in proportion to fork length raised to the power of 3.03, territory size increased in proportion to $M^{0.82-0.86}$ (2.48/3.03 − 2.61/3.03). In salmonids, metabolic rate is proportional to M raised to exponents between 0.75 and 1.10 (Brett 1965; Brett and Glass 1973; Schmidt–Nielsen 1984) rather than the ubiquitous exponent of 0.75 (Peters 1983). Therefore, Fig. 1 was consistent with the hypothesis that juvenile salmonids increase their territory size as they grow in proportion to their increasing energetic requirements.

Unlike salmonids, the home range/territory size — body mass relationships for birds, mammals, and lizards have greater exponents than their corresponding metabolic rate — body size relationships (Harestad and Bunnell 1979; Calder 1984; Lindstedt et al. 1986). Damuth (1981) suggests that the greater than expected slopes occur because the number of conspecifics that share a home range increases with increasing body size, at least for herbivorous mammals. Salmonids are unique in a number of ways that may account for the apparent difference in the allometry of their territories. They defend relatively two-dimensional territories near the stream bottom, and yet feed throughout the water column on drifting aquatic invertebrates. Hence, the productivity of a salmonid territory will be directly proportional to the cross-sectional area of the territory or the square root of territory area. However, larger salmonids tend to occupy faster and deeper water (Chapman and Bjornn 1969), both of which will increase the food production of a territory. In addition, range overlap will be independent of body size because salmonids defend relatively exclusive territories. Thus, even if salmonid territory size increases in direct proportion to metabolic requirements, it is not clear how they should scale to body size.

Juvenile salmonids defend territories of about seven body lengths in diameter (Grant et al. 1989). Compared to data for birds (Schoener 1968), salmonid territories [$\log_{10}$ area (m^2) = 0.86 $\log_{10} M$ (g) − 1.17] are five orders of magnitude smaller than bird territories [$\log_{10}$ area (m^2) = 1.14 $\log_{10} M$ (g) + 4.00]. The only other data available for poikilotherms, suggest that the home range size of lizards ($\log_{10}$ area (m^2) = 0.95 $\log_{10} M$ (g) + 3.12) are four orders of magnitude larger than salmonid territories (Turner et al. 1969). Thus, the territory–size hypothesis predicts that the maximum densities of stream-dwelling salmonids will be much higher than those of most animals of comparable size (see Peters 1983, chapter 10).

Some of the variation about the interspecific regression may reflect species differences, different methods of measuring territory size, and stochastic variation related to small sample sizes. The mean square error about the interspecific regression was 0.066 compared to 0.089 for the brook trout regression in Fig. 1 and 0.253 for a brook trout regression for 110 less frequently aggressive fish (Grant et al. 1989). Hence, there was considerable variation about the brook trout regressions, even

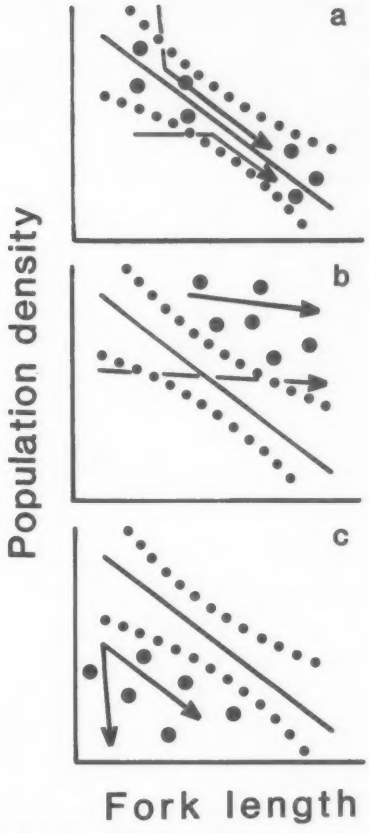

FIG. 2. Hypothetical population density data from single samples (dots) or from following cohorts through time (arrows) in relation to the maximum-density regression (solid line) and its 95% C.L. (dotted lines), predicted by the inverse of the territory–size regression. The data in (a) strongly support the hypothesis that territoriality limits density, whereas those in (b) falsify the hypothesis, and those in (c) suggest the hypothesis is irrelevant.

when the effects of species and methodology were removed. We suspect this variation is real and is related to factors such as food density, intruder pressure, current velocity, and water depth. Including these factors in a multiple regression would potentially decrease the variation about the allometric regressions, but the data are not currently available to do this.

Territory Size and the Limitation of Population Density

Predictions of the Territory-Size Hypothesis

When a single size-class of fish occupies a habitat, the territory–size hypothesis predicts that their maximum density will be the inverse of their territory size predicted from the territory–size regression. To test this prediction, we compared population density data from the literature to the maximum-density regression (i.e. the inverse of the territory–size regression):

$$\log_{10} \text{density} = -2.61 \log_{10} \text{fork length} + 2.83.$$

In Fig. 2 we show how we would use three hypothetical data sets to test this prediction. The arrows represent cohorts of fish that are sampled repeatedly through time. An arrow moving horizontally to the right indicates growth of fish with no mortality whereas an arrow moving vertically down indicates mortality or emigration with no growth. Dots represent single population samples.

The territory–size hypothesis predicts that a cohort beginning above the regression will move steeply down and then follow a trajectory along the maximum-density regression (Fig. 2a), that a cohort beginning below the regression will initially move horizontally and then follow a trajectory along the maximum-density regression, and that individual data points will cluster about the maximum-density regression within the 95% C.L. The territory–size hypothesis would be falsified by a cohort that begins and remains above the maximum-density regression, by a cohort that begins below and crosses above the regression, or by individual data points consistently above the upper 95% C.L. (Fig. 2b). Cohorts that begin below and do not approach the maximum–density regression (Fig. 2c) do not falsify the hypothesis but suggest that it is irrelevant. Other factors such as food, predation, or the quality of habitat must be limiting density. We would draw a similar conclusion if individual data points were consistently below the lower 95% C.L. of the maximum–density regression.

The simple graphical test of the hypothesis (Fig. 2) cannot be used when more than one size-class of fish is present in the habitat unit that is sampled for population density. Instead, we used the territory–size regression to calculate an index of habitat saturation. For fish of size i, maximum density (D_i max) was calculated from the maximum-density regression; this maximum density was defined as 100% saturated. For populations with n cohorts or size-classes present at one time, percent habitat saturation (PHS) was calculated as:

$$\text{PHS} = 100 \cdot \sum_{i=1}^{n} D_i/D_i \text{ max},$$

$$= 100 \cdot \sum_{i=1}^{n} D_i \cdot T_i \cdot 1.19,$$

where D_i is the actual density (per m^2) of size-class i, T_i is the territory size (m^2) for size-class i predicted from the territory size — body size regression, and 1.19 is a correction factor that is needed to remove bias introduced when the data were $\log_{10}$ transformed (Sprugel 1983). If different size-classes do not have overlapping territories, due either to habitat segregation by size or to defence against all size-classes, then the territory–size hypothesis predicts that the maximum PHS will be 100. However, if territories of different size-classes overlap, i.e. no defence between size-classes, then PHS could be greater than 100.

The abundance of salmonids in streams is often reported as biomass ($g \cdot m^{-2}$) or production ($g \cdot m^{-2} \cdot yr^{-1}$), neither of which can be used to test the predictions in Fig. 2. However, if $\log_{10}$ maximum density (no.$\cdot m^{-2}$) = 2.83 − 2.61 $\log_{10}$ fork length (cm) (i.e. the inverse of the territory–size regression in Fig. 1), and $\log_{10}$ mass = 3.03 $\log_{10}$ fork length − 1.93 (see Methods) then $\log_{10}$ biomass ($g \cdot m^{-2}$) = 0.42 $\log_{10}$ fork length + 0.90. This implies that the biomass of salmonids in cultures of uniform size will increase with body length. For salmonids of 23 cm, the largest fish in our interspecific regression (Table 1), the predicted biomass is 30 $g \cdot m^{-2}$. We can use this as a rough

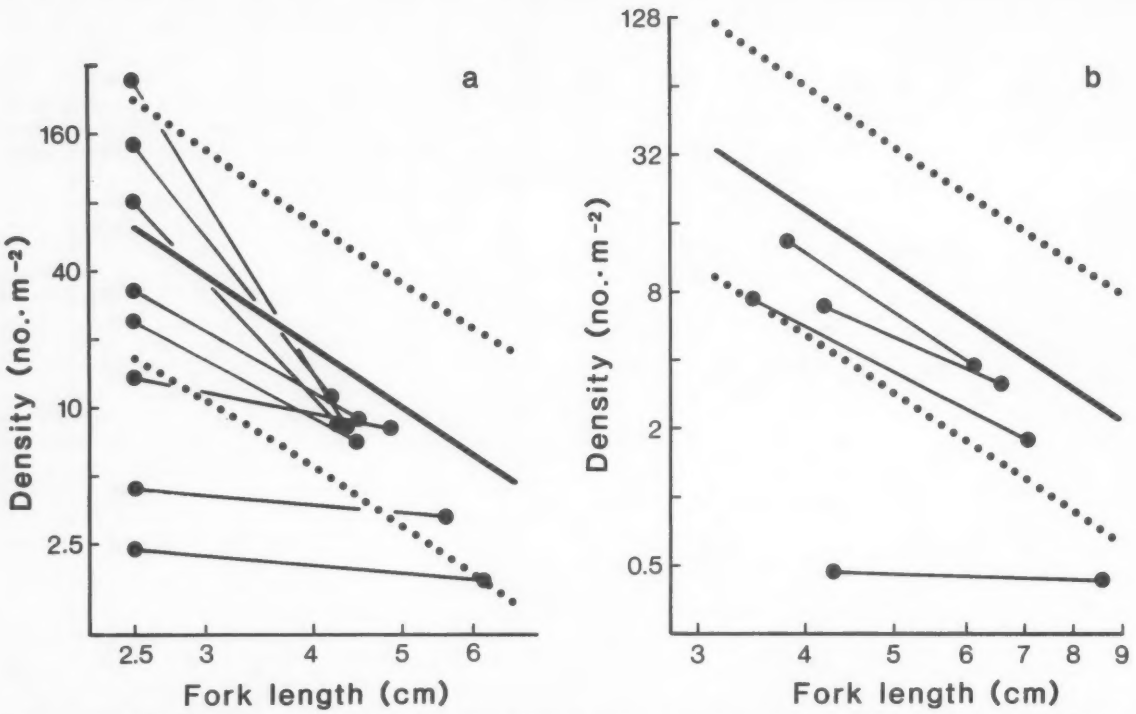

FIG. 3. (a) Population density and mean size of 0+ brown trout stocked in cages or screened sections of streams and recovered 133 d later (Le Cren 1965, 1973). Lines join the initial population to the recovered population. The heavy line is the maximum-density regression with 95% C.L. for individual predicted values. (b) Total population density and mean size of juvenile coho salmon and steelhead trout stocked and recovered in artificial stream channels (Fraser 1969). Lines join the initial and final populations after a 163 d experiment.

estimate of the predicted maximum biomass of salmonids in streams.

Methods

The clearest data for testing the hypothesis come from experimental studies that follow a single cohort of fish through time. These studies typically provide relatively uniform habitats and accurate estimates of fish size and density. Experimental studies are presented in detail in the results if a single size-class of fish was stocked at a variety of densities and followed for at least 1 mo. Studies are presented in less detail if more than one size-class of fish was used, the fish were stocked at a single or small range of densities, or the fish were followed for less than 1 mo.

Non-experimental data are also important because they reflect densities of fish under natural conditions. These observational data are of three types: local-habitat densities, average-stream densities, and average-stream biomass. Local-habitat densities are the most relevant of the three types for testing the hypothesis. Because of habitat patchiness, some areas of the stream bed will be unsuitable for stream-dwelling salmonids in general or for a particular size-class of fish. By focussing on smaller sampling units, local-habitat densities restrict the size range of fish per sample, which facilitates graphical testing of the hypothesis (i.e. Fig. 2). In addition, smaller sampling units increase the range and hence maximum densities encountered (Krebs 1989, chapter 3); the latter are important for testing the hypothesis.

Most local-habitat densities in the literature are from focal-animal observations (Altmann 1974). By definition, these data exclude unused and low-density habitats, thereby providing the maximum densities in suitable habitats. As part of a study of the social behaviour of young-of-the-year brook trout (see Grant and Noakes 1988), the number of conspecifics was counted within a 1 m^2 area around the focal fish. We searched the literature for similar data for other species.

Because average stream-density data are less satisfactory for testing the predictions of Fig. 2, we included only those originally presented by Allen (1969) and the exceptional 17-yr data set for Black Brows Beck (Elliott 1984a, 1984b, 1985, 1987, 1988).

Because they ignore the distribution of mass among individuals, average-stream biomass were the least relevant of the three types of observational data for testing the predictions of Fig. 2. Hence, we rely primarily on data in a recent review by Mann and Penczak (1986).

Results

Experimental studies

Le Cren (1965, 1973) — Le Cren stocked brown trout alevins into small screened sections of a natural stream and counted the survivors 133 d later. The trout fed on natural food that drifted into the sections. Le Cren's original data provided strong evidence of a flat-topped stock-recruitment curve, which led him to conclude that territorial behaviour was responsible for

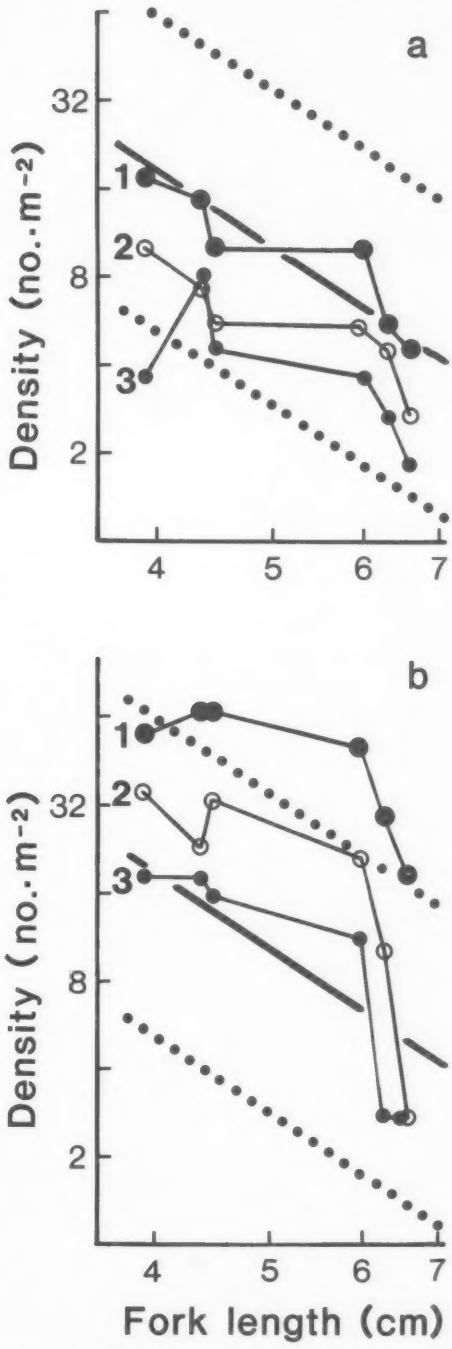

FIG. 4. Population density and mean size of juvenile coho salmon in (a) 3 riffles and (b) 3 pools of an artificial stream channel (Mason and Chapman 1965). The lines follow the number of fish in each compartment over a 4-mo experiment. The numbers refer to riffles 1, 2, and 3 and pools 1, 2, and 3 respectively (1 is upstream, 3 is downstream). The solid and dotted lines are as in Fig. 3.

the density-dependent starvation. Le Cren reported weights but not lengths of fish so we used Elliott's (1984b) relationship for brown trout to estimate length.

When Le Cren's data are replotted with our maximum-density regression, they provide strong support for the territory–size hypothesis (Fig. 3a). When initial densities were above the line, the number of survivors was just below that predicted by the maximum-density regression. When initial densities were well below the line, the cohort trajectories were virtually horizontal.

Fraser (1969) — Fraser stocked a mixture of juvenile coho salmon and rainbow trout into stream channels from which they could not emigrate, and counted the survivors 163 d later. The cause of death was unknown. The fish fed on natural drift entering and produced within the channel. Growth rate and survival rate of fish decreased with increasing density.

Fraser's data (Fig. 3b) were consistent with the hypothesis in Fig. 2a. At the three highest stocking densities, the cohort trajectories paralleled the maximum-density regression. When the stocking density was well below the line, the cohort trajectory was horizontal.

Mason and Chapman (1965) — Mason and Chapman stocked 300 coho salmon alevins into two stream channels that were each divided into six habitats: three riffles alternating with three pools. The coho salmon could move freely among the habitats or emigrate from the channel. Food entered the channel as natural drift at the upstream end (riffle 1, pool 1); drift density decreased downstream as the fish removed drift from the water. The number of fish was followed for 4 mo. Only data for the left channel are presented in detail (see their table III). The alevins in the right channel emerged from the gravel asynchronously, and therefore were considered in less detail below. Fork length was estimated from data in their table V.

Mason and Chapman's (1965) data for the three riffles (Fig. 4a) and three pools (Fig. 4b) are replotted with our regression. There were no significant differences among the slopes of regressions through the seven data sets ($P = 0.65$, ANCOVA), but the intercepts were different ($P < 0.0001$). The adjusted mean density for riffle 1 was not significantly different from the maximum-density regression ($P = 0.97$, ANCOVA) and provided strong support for the territory–size hypothesis. Adjusted mean densities for riffle 2 and 3 were less than the maximum-density regression ($P = 0.027$ and 0.0002, respectively), demonstrating the infuence of food availability on population density.

Data for pools 1 and 2 falsified the territory–size hypothesis since the adjusted mean density of coho salmon was greater than the maximum-density regression ($P = 0.0001$ and 0.025, respectively). The densities of coho salmon in pool habitats of Mason's (1969) experiments (not shown) were also above the upper 95% C.L. Food availability was also important in pools as population density decreased from pool 1 to pool 3 ($P = 0.0003$, ANCOVA).

Mason and Chapman's (1965) data also illustrate the importance of measuring local-habitat density rather than average-stream density for composite habitats. Even within this small stream channel (7.6 × 0.9 m), the density varied by an order of magnitude between pool 1 and riffle 3 (Fig. 4a, 4b).

Mason (1976) — Mason's influential study attempted to determine whether food or space limited the density of stream-dwelling salmonids during summer. Mason stocked juvenile coho salmon into small screened sections of a natural stream under two feeding regimes: natural food only or natural food

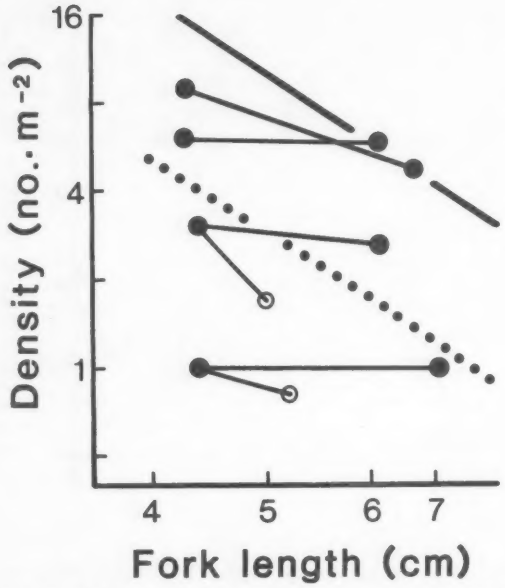

FIG. 5. Population density and mean size of coho salmon stocked and recovered from screened sections of a natural stream (Mason 1976). Solid circles show populations recovered from sections supplemented with food; the open circles show control populations. The solid line is the maximum-density regression with the lower 95% C.L.

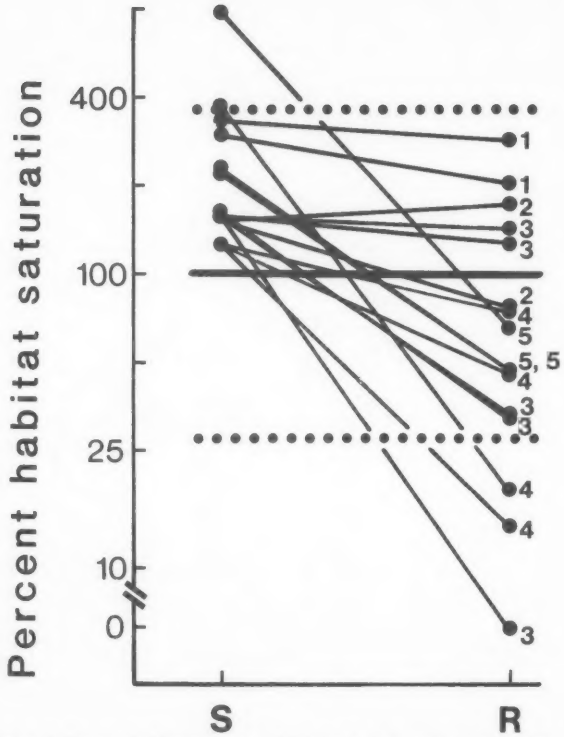

FIG. 6. Percent habitat saturation for juvenile salmonids stocked (S) and non-emigrants recovered (R) in experimental laboratory studies. Numbers refer to data from (1) Fausch (1984), (2) right riffle 1 and 2 from Mason and Chapman (1965), (3) Wilzbach (1985), (4) Slaney and Northcote (1974), and (5) Stein et al. (1972). The solid line represents a PHS of 100; the dotted lines are the approximate 95% C.L. from the maximum-density regression.

supplemented with a daily ration of 15% per day. Fish were allowed to emigrate from the sections, and the number of survivors was recovered after either 50 or 62 d.

Supplemental feeding of coho salmon increased the growth rate and density of fish remaining in the sections compared to control populations (Fig. 5). Mason concluded that food and not space limited the density of juvenile coho. However, his results were also consistent with the territory–size hypothesis because the density of fish recovered from the two highest stocking densities were very close to the maximum-density line. Repeating these experiments at higher stocking densities and food densities would provide a stronger test of the territory–size hypothesis.

Other experimental studies — A number of authors stocked juvenile salmonids in stream tanks at high density, allowed some to emigrate, and reported "final" densities when emigration had ceased. We have collected these data in Fig. 6. To allow us to present all the data in one figure, the data are expressed as percent habitat saturation (PHS).

The data were generally consistent with the predictions since 13 of 16 recovered populations were within the 95% C.L. Ten of 16 populations were below saturation, but this did not differ from chance ($P>0.20$, two-tailed binomial test). The variation in PHS of the final populations was probably due to factors other than just space. For example, all 10 fish emigrated from the low food + high cover treatment of Wilzbach's (1985) experiment. Of particular interest are the two data points of Fausch (1984). His initial densities were close to the upper 95% C.L. and although emigration occurred, the final densities were well above 100 PHS, but within the C.L. However, 87% of the fish remaining in the stream channels lost weight during his experiment. Thus, fewer fish than expected emigrated, but they showed the effects of space-related competition by losing weight. These fish would presumably starve to death in a longer-term experiment that allowed no emigration.

Observational studies

Local-habitat density — Population density of young-of-the-year brook trout from three streams in southern Ontario are plotted in Fig. 7 (J. W. A. Grant, unpubl. data); the range in size is due to growth over the summer. Young-of-the-year trout rarely used the same microhabitat as older age-classes in these streams, so the data represent the total standing crop in these habitats. No density exceeded the upper 95% C.L. The density of small fish (<4 cm) was more often (76%) below the lower 95% C.L. than was the density of large fish (15%). The trajectory of the points was consistent with the predictions of Fig. 2a. The density of small trout did not appear to be limited by territory size, whereas space appeared to be more limiting for large young-of-the-year trout.

Other visual estimates of local-habitat density from the literature are shown in Fig. 8. Most of the points are within the 95% C.L. of the maximum-density regression. Of note are the data of Puckett and Dill (1985) who observed "floaters" living between the territories of other fish (point 4). If these floaters are excess fish that cannot acquire a permanent territory, then the population density of territorial fish alone (point 3) should be close to saturation. The large range in density of territorial

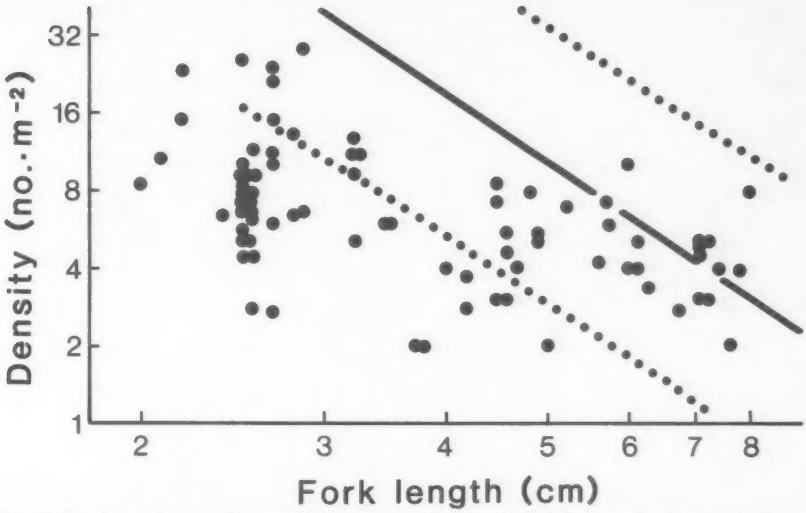

FIG. 7. Population density of young-of-the-year brook trout estimated from focal-animal observations in three southern Ontario streams. Each point represents the mean density of 1 d in one stream. The range in size is due to growth over the summer. Solid and dotted lines as in Fig. 3.

fish suggested that floaters might not always be individuals that cannot acquire a territory because of a lack of space, but rather are individuals that adopt an alternative foraging strategy. The total density of territorial fish plus floaters (point 5) was close to the regression line, supporting this latter interpretation.

Average-stream density — Allen (1969) collated density data for salmonids in streams from the literature. These data (Fig. 9) represent higher than average densities because Allen rejected studies where densities were so low as to suggest that factors other than space were limiting.

Sixteen of the 20 data points were below the lower 95% C.L. and the mean PHS was 18.6 (range = 4.5–68.6). If these data accurately represent higher than average densities of salmonids in the wild, then we would conclude that other factors such as food, spawning habitat, or predation must normally limit these populations. However, we think these data underestimate the actual density of fish in usuable habitat because Allen (1969) deliberately combined data for separate stream sections to obtain average densities for large areas of stream. Furthermore, Allen plotted data for different size-classes in the same area separately. Different size-classes in the same area should be summed unless they occupy different microhabitats and densities are reported separately for those microhabitats. Otherwise, one needs an estimate of the total space used by all size-classes in the area sampled for population density. When we summed the densities of different size classes in an area, only four of 10 points fell below the lower 95% C.L., the mean PHS was 37.2 (range = 11.3–71.9), and none were above the upper 95% C.L. Hence, Allen's revised data were generally consistent with the territory–size hypothesis.

Elliott (1984a) measured the density of juvenile brown trout in Black Brows Beck, England for 17 consecutive years. There was strong density-dependent mortality within the first 2 mo after emergence when young trout were establishing feeding territories (Elliott 1984). When we replotted these data (Fig. 10) the density of emerging alevins was close to the regression. The steep drop in density reflects the strong density-dependent mortality observed by Elliott, after which the cohort trajectory follows the lower 95% C.L. of the maximum-density line. The sharp drop in density after emergence is qualitatively consistent with the territory–size hypothesis, but these data underestimate total fish density because there was more than one year-class present at a time.

To present graphically more than one cohort at a time, we plotted PHS for all fish that were present at one time (Fig. 11); this was possible for 14 yr. For the May/June and Aug./Sept. samples, we summed the PHS for the 0+, 1+, and 2+ cohorts. Elliott did not sample the 1+ and 2+ cohorts during the emergence of 0+ fish, so we assumed that PHS for these fish did not change between emergence in April and the first sampling in May/June, i.e. that any growth during this short period was offset by mortality. The decrease in PHS between April and May/June was due entirely to the death of 0+ trout. All cohorts were below 100 in May/June ($P = 0.002$, two-tailed binomial test), suggesting that the density-dependent mortality of 0+ trout overcompensated for the high density of alevins in April. However, the trout population responded to this overshoot as 13 of 14 cohorts increased in PHS between May/June and Aug./Sept. Eleven cohorts remained below saturation at the Aug./Sept. census ($P = 0.057$, two tailed binomial test).

All the points in the May/June and Aug./Sept. samples were within the 95% C.L. and clustered closely about the territory-size line. Hence, Elliott's data appear to provide strong support for the hypothesis.

Biomass data — An extensive review of salmonid biomass is beyond the scope of this paper, but Mann and Penczak (1986), who recently reviewed salmonid production in 85 streams, concluded that an approximate ceiling in production occurs at about 30 $g \cdot m^{-2} \cdot yr^{-1}$. Assuming an average production/biomass ratio of 1.30 (Mann and Penczak 1986), this translates to a maximum biomass of 23 $g \cdot m^{-2}$, not far below our predicted maximum of 30 $g \cdot m^{-2}$. We are aware of two studies that exceed 30 $g \cdot m^{-2}$. Sand Creek, Wyoming, had a biomass of 63.4 $g \cdot m^{-2}$; the biomass in the remaining 43 streams surveyed by Binns and Eiserman (1979) was less than 30 $g \cdot m^{-2}$. The biomass of brown trout in the Horokiwi stream apparently

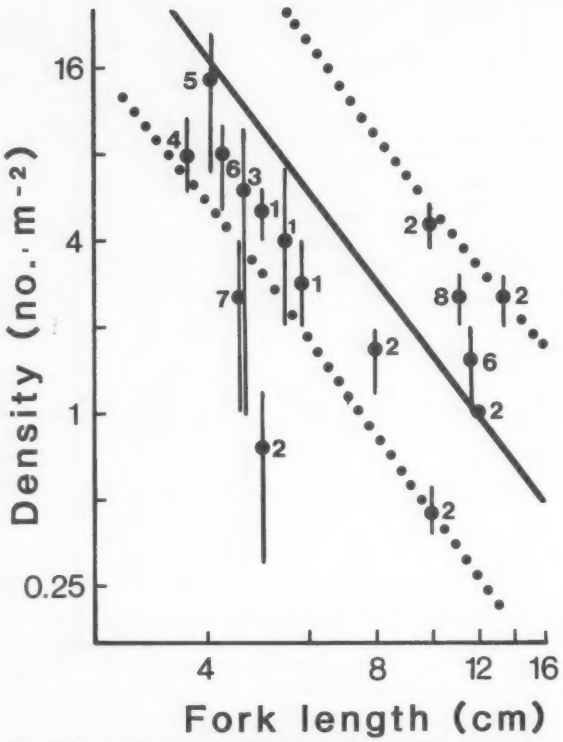

FIG. 8. Local-habitat densities (mean and range) of stream-dwelling salmonids from visual surveys. The numbers refer to data from the following papers: (1) Chapman (1962), (2) Wankowski and Thorpe (1979), (3) territorial fish, Puckett and Dill (1985), (4) floaters, Puckett and Dill (1985), (5) territorial fish + floaters, Puckett and Dill (1985), (6) nonterritorial fish, Puckett and Dill (1985), (7) McNicol et al. (1985), and (8) Stradmeyer and Thorpe (1987). Solid and dotted lines as in Fig. 3.

exceeds 50 $g \cdot m^{-2}$, but Le Cren (1969) suggests that this value is an overestimate. Given the approximations in the calculations, neither estimate is far above the suggested maximum. Moreover, higher values would be expected if fish were larger than 23 cm or if pools were common at a site (see below).

Discussion

The territory–size hypothesis was clearly falsified in the pool habitats of Mason's (Mason and Chapman 1965; Mason 1969) stream channel. The coho salmon in these pools were distributed throughout the water column (also see Fausch and White 1986), but were found only near the substrate in riffles (see figures 9 and 10 in Mason (1969)). This falsification suggests that the hypothesis is not applicable in three-dimensional habitats such as pools. Apparently, more fish than predicted by the maximum-density regression can occupy sites if the fish are distributed in three dimensions. If the same pattern occurs in natural streams, then we would predict high standing crops of salmonids in pool habitats. There is some evidence of this: salmonid biomass was positively correlated with the percentage of stream area that was composed of pools (Bowlby and Roff 1986) and pool volume (Nickelson et al. 1979 in Fausch et al. 1988).

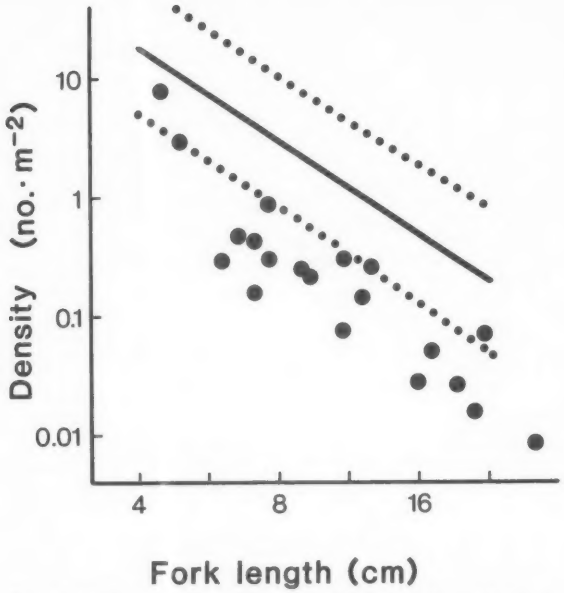

FIG. 9. Average-stream density for resident populations of stream-dwelling salmonids from table 1 of Allen (1969). Solid and dotted lines as in Fig. 3.

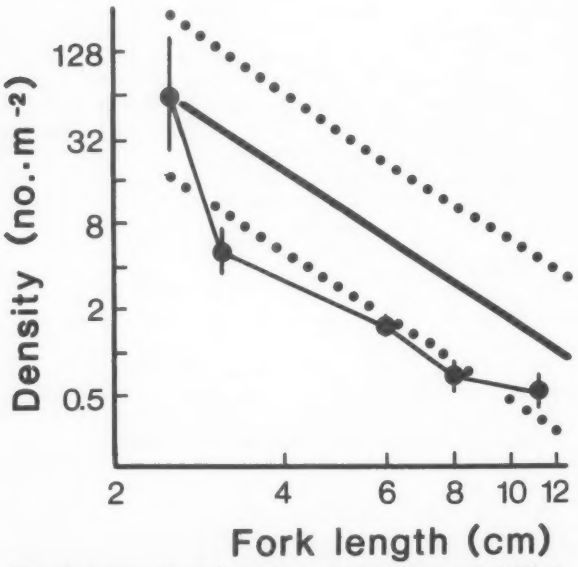

FIG. 10. Average-stream density (mean and SD) of brown trout in Black Brow's Beck (Elliott 1984a, 1984b, 1985). Successive points follow cohorts from emergence as alevins, to 0+ in May, to 0+ in August, to 1+ the folowing May, to 1+ the following August. Solid and dotted lines as in Fig. 3.

When the comparisons are limited to shallow habitats, many of the experimental data (e.g. Fig. 3, 4a) and field data (e.g. Fig. 7, 8, 11) were consistent with the territory–size hypothesis and no data provided a clear falsification. However, more field estimates of local fish density in usable habitat are needed to test the hypothesis more rigorously.

TABLE 2. Studies reporting density-dependent or no density-dependent responses in relation to percent habitat saturation (PHS) calculated from the territory–size regression.

Source[a]	Age-class[b]	Species[c]	Comparison	PHS		Response[d]		
				Mean	Range	G	M	E
1	0+	*O.k.*	single density	161				+
1	0+	*O.k.*	single density	83				+
1	0+	*O.k.*	single density	14				—
2	0+	*S.s.*	different years	105	71–129	+	+	
3	0+	*S.s.*	different densities	56	35–107	+	+	
4,5,6	0+	*S.t.*	different years	74	41–115	—	+	
7,8	M	*S.t.*	different years	44	27–56	—	—	
9	M	*S.t.*	single density	298				+
9	M	*O.k.*	single density	329				+
10	0+	*O.k.*, *O.m.*	different densities	41	4–78	+	+	
11,12	M	*S.s.*	different stream sections	27	6–41	—	+	
13	0+	*S.s.*, *O.m.*	effect of *S.s.* on *O.m.*	19				—
13	0+	*O.m.*	single density	13				—
14	1+	*S.f.*	different years	43	35–52	+	+	
15	0+	*S.t.*	effect of *S.s.* on *S.t.*	49	42–57	+		
15	M	*S.t.*, *S.s.*	different years	63	57–69	+	+	
15	0+	*S.t.*	different years	37	28–42	—		
16	0+	*S.s.*	effect of *S.t.* on *S.s.*	68	59–76	+		
16	M	*S.s.*	different years	69	54–83	+	+	
17,18	0+	*S.t.*	different densities	140	5–535	+	+	
19	M	*O.m.*	different densities	404	135–673	+		
20	0+	*O.k.*	single density	273				+
20	0+	*O.k.*	single density	405				+
20	0+	*O.k.*	single density	79				—
20	0+	*O.k.*	single density	209				+
21	0+	*O.k.*	different densities, unfed	17	8–27	+		
21	0+	*O.k.*	single density	24				+
21	0+	*O.k.*	single density	48				+
21	0+	*O.k.*	single density	8				—
21	0+	*O.k.*	single density	24				—
21	0+	*O.k.*	single density	71				—
22	0+	*O.k.*	single density	137				+
22	0+	*O.k.*	single density	151				+
23	1+	*S.f.*	different years	41	32–55	—	+	
24	0+	*S.s.*	different densities	23	13–44	+	—	
25	0+	*S.t.*	different stream sections	20	6–35		+	
26	M	*S.s.*	different stream sections	9	4–12	—		
26	M	*S.s.*	different stream sections	5	3–8	—		
27	0+	*O.k.*	single density	74				+
27	0+	*O.k.*	single density	53				+
27	0+	*O.k.*	single density	86				+
27	0+	*O.k.*	single density	61				+
28	0+	*S.f.*	different years, Hunt Creek	17	15–22		+	
28	0+	*S.f.*	different densities	20	9–36		—	
29	0+	*O.m.*	single density	368				+
29	0+	*O.m.*	single density	127				+
29	0+	*O.m.*	equilibrium density	18				—
30	0+	*O.k.*, *O.t.*	single density	775				+
30	0+	*O.k.*, *O.t.*	single density	227				+
30	0+	*O.k.*, *O.t.*	single density	218				+
30	0+	*O.k.*, *O.t.*	single density	82				+
30	0+	*O.k.*, *O.t.*	single density	56				+
31	M	*O.c.*	single density	156				+

[a]1 = Chapman 1962; 2, 3 = Egglishaw and Shackley 1977, 1980; 4, 5, 6, 7, 8 = Elliott 1984a, 1984b, 1985, 1987, 1988; 9 = Fausch 1984; 10 = Fraser 1969; 11, 12 = Gee et al. 1978a, b; 13 = Hearn and Kynard 1986; 14 = Hunt 1974; 15, 16 = Kennedy and Strange 1980, 1986; 17, 18 = Le Cren 1965, 1973; 19 = Li and Brocksen 1977; 20, 21 = Mason 1969, 1976; 22 = Mason and Chapman 1965; 23 = McFadden et al. 1967; 24 = Mills 1969; 25 Mortensen 1977; 26 = Randall and Chadwick 1986; 27 = Ruggles 1966; 28 = Shetter 1961; 29 = Slaney and Northcote 1974; 30 = Stein et al. 1972; 31 = Wilzbach 1985.

[b]M = more than one age-class.

[c]*O.k.* = coho salmon, *O.t.* = chinook salmon, *O.m.* = rainbow trout, *O.c.* = cutthroat trout, *S.s.* = Atlantic salmon, *S.t.* = brown trout, and *S.f.* = brook trout.

[d]G = growth rate, M = mortality rate, E = emigration rate; + = a significant decrease in growth rate or an increase in mortality rate with increasing density or more than 10% of the fish emigrated; — = no significant changes in growth or mortality rate with changes in density or less than 10% of the fish emigrated.

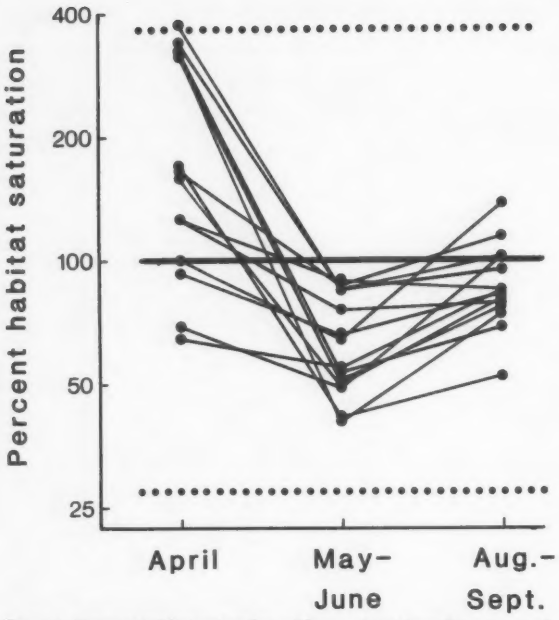

FIG. 11. Percent habitat saturation of brown trout (age 0+, 1+ and 2+) in Black Brow's Beck (Elliott 1984a, 1984b, 1985). Solid and dotted lines as in Fig. 6.

Although the data show that the territory–size regression can be used to predict maximum densities of stream-dwelling salmonids, this cannot be taken as evidence that territoriality is the actual mechanism that limits density. Not all individuals defend territories in the field (Puckett and Dill 1985; Grant and Noakes 1988) or even in some of the experimental studies that provided strong support for the territory–size hypothesis (e.g. riffle 1, Mason and Chapman 1965; Slaney and Northcote 1974; Fausch 1984). Hence, population density reported in many studies probably includes floaters or other individuals that do not defend space. We suspect that territoriality per se is not the mechanism that limits density, but rather that territory size predicts the spatial requirements of stream-dwelling salmonids, whether the space is defended or not. In territorial brook trout, foraging areas were similar to defended areas (Grant et al. 1989). Nonterritorial brook trout in the same streams had somewhat smaller foraging areas than territorial fish (Grant 1990), but their foraging areas may be sufficiently similar in size to be adequately predicted by the territory–size regression. When these spatial requirements are not met, density-dependent growth, mortality, or emigration should occur.

Territory–Size Hypothesis and Density-Dependent Responses

Predictions

The territory–size hypothesis predicts the maximum densities of stream-dwelling salmoids. As a cohort approaches this saturation point, the hypothesis predicts that individuals will cease growing, emigrate or die. If space is the only factor affecting growth, emigration, and mortality, then the territory–size hypothesis predicts that these responses will be density-independent at densities below the lower 95% C.L. of the maximum-density regression. As the habitat becomes increasingly saturated, the probability of observing density-dependent responses increases until it reaches 1.0 at a habitat saturation of 100%. If factors other than space affect growth, emigration, and mortality, then density-dependent responses can occur at densities less than the lower 95% C.L. of the maximum-density regression. However, the qualitative prediction of the territory–size hypothesis will still hold: the probability of observing a density-dependent response increases with increasing density or habitat saturation. It is also important for fisheries managers to know at what densities or levels of habitat saturation these responses occur.

Methods

To test the predictions of the territory–size hypothesis, we searched the literature for studies that reported either density-dependent or no density-dependent responses. A density-dependent response was defined as a statistically significant ($P<0.05$) decrease in growth rate or increase in mortality rate with increasing density, or as emigration by more than 10% of the fish. 'No emigration' was defined as less than 10% of the initial fish leaving to guard against a few individuals reacting abnormally to laboratory conditions or a low level of density-independent emigration in the field. Emigration was the most sensitive measure of density-dependent responses because we could score a response for a specific value of PHS. In contrast, we could only assess density-dependent growth or mortality by a significant change in the response at different values of PHS.

Many of the populations could be scored (yes or no) for more than one of the three potential responses: growth, mortality, and emigration. To insure independence of the data, a population contributed only one data point if it showed the same response for all measures. Populations that showed ambiguous responses (e.g. two yes, one no; one yes, two no; one yes, one no) contributed two data points: one yes and one no.

Results

Table 2 lists studies that report either density-dependent or no significant density-dependent responses in relation to PHS. Because we could not score the strength of a density-dependent response for all studies, we treated it as a categorical response: yes or no. There are as yet too few data to draw strong conclusions about whether growth, mortality, and emigration respond differently to increases in PHS. One interesting trend was that three studies that reported strong density-dependent mortality reported no density-dependent growth (McFadden et al. 1967; Gee et al. 1978a, b; Elliott 1984a, b).

We used PHS to predict whether or not density-dependent responses occurred: a datum was included for each row in Table 2. Because PHS is a continuous variable and density-dependence is a categorical variable, we analyzed the data using a linear logistic response model (Fienberg 1980; also called logistic regression, SAS Institute Inc. 1982). As predicted by the territory–size hypothesis, the probability of observing a density-dependent response increased with increasing mean PHS (Fig. 12). The logistic response function correctly predicted the response in 81% (46/57) of the cases (Fig. 12).

The inflection point in the response function represents the equal probability of observing density-dependent and no density-dependent responses. The PHS at the inflection point (27.2) was remarkably close to the lower 95% C.L. of the maximum-density regression (PHS = 27.8). At a PHS of 100, the

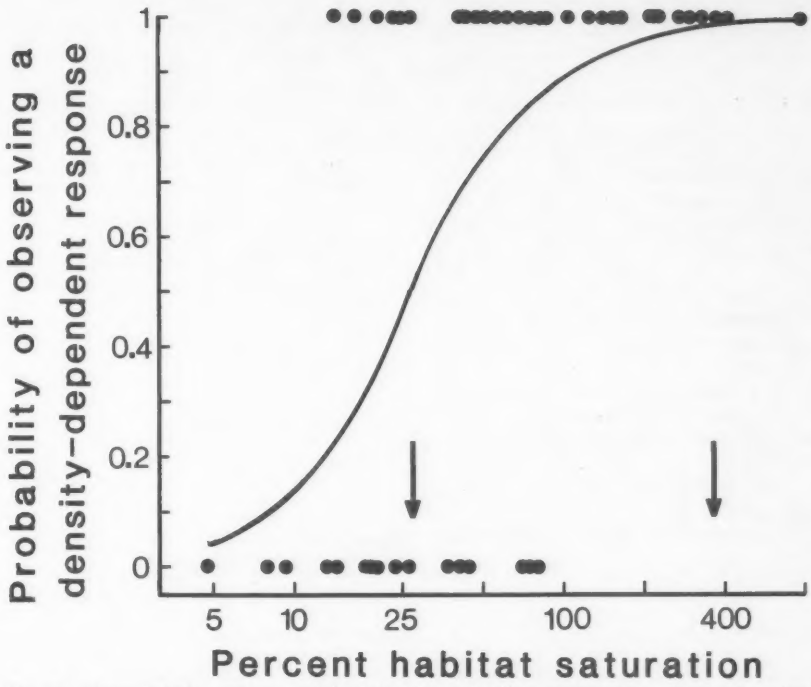

FIG. 12. Linear logistic response model relating the probability of observing a density-dependent response (growth, mortality, or emigration) in relation to percent habitat saturation (PHS). The line is $\ln(p/1-p) = 4.07 \log_{10} \text{PHS} - 5.84$, where p = probability of observing a density-dependent response ($\chi^2 = 12.16$, $n = 57$, df = 1, $P<0.001$). The inflection point ($P = 0.5$) is at a PHS of 27.2; the arrows show the approximate 95% C.L. of the territory–size regression. Individual data points are shown ($P = 0$ or $P = 1.0$).

logistic response function predicted that the probability of observing a density-dependent response was 0.91.

Discussion

The accuracy with which mean PHS was able to predict the occurrence of density-dependent responses (81%) was encouraging because PHS is a measure only of the spatial saturation of the habitat; we deliberately ignored other important factors like habitat productivity and predation which undoubtedly affect growth, mortality, and emigration. In addition, we have ignored the quality of the habitat and assumed that all space used by the fish is equivalent. The predictive power of PHS would probably increase if one could apply the technique only to suitable habitat (sensu Bovee 1982) for a given species or life stage or incorporate other factors in a multiple regression.

The close correspondance between the inflection point in the logistic regression and the lower 95% C.L. suggested that the territory–size regression delimits a zone of space-related competition. We believe that the territory–size regression and the concept of PHS have applied value for salmonid biologists. Percent habitat saturation may be a valuable index for comparing the density or standing crop between streams or within streams over years. Abundance is traditionally expressed as density (no.·m^{-2}) or as biomass (g·m^{-2}), thus ignoring the size of the fish. Biomass data integrate the number and size of fish but assume that the distribution of mass among individuals is not important. The territory–size hypothesis predicts that this would not be the case: more space is used by two 1-g fish than by one 2-g fish. PHS provides an index that integrates the number, size, and space requirements of salmonid fish.

The territory–size regression and PHS can be used as rough guides for setting maximum stocking densities for stream-dwelling salmonids in relation to body size. For example, the logistic response function suggests that stocking fish into a stream where the PHS of the resident populations is greater than 27 will likely cause a density-dependent response in either the stocked or resident population.

The territory–size hypothesis predicts that a cohort of stream-dwelling salmonids in a saturated environment will experience a reduction in population density as individuals increase in size. This "self-thinning" phenomenon has been widely studied in plants (Westoby 1984) and recently in sessible marine invertebrates (Hughes and Griffiths 1988). Double logarithmic regressions of average plant mass vs. plant density often, but not always, have a slope close to -3/2 (Weller 1987). Based on energetic allometries, Begon et al. (1986) have argued that mobile animal populations should exhibit a self-thinning slope of $-4/3$. Our empirical regressions suggested a slope of -1.16 for stream-dwelling salmonids. If $\log_{10}$ density $= 2.83 - 2.61 \log_{10}$ fork length, and $\log_{10}$ mass $= 3.03 \log_{10}$ fork length $- 1.93$, then $\log_{10}$ mass $= 1.35 - 1.16 \log_{10}$ density. The validity of this salmonid thinning line remains to be tested.

Conclusions

Body length explained 87% of the variation in territory size of juvenile salmonids in streams, despite differences in species,

environmental conditions, and methods of measuring territory size. We used the inverse of this regression, the maximum-density regression, to test the hypothesis that territory size limits the maximum density of juvenile salmonids in streams. In shallow habitats such as riffles and raceways, no data clearly falsified the hypothesis and most either strongly supported or were consistent with the territory-size hypothesis. We suspect that territoriality is not the mechanism that actually limits density, but rather that territory size predicts the spatial requirements of stream-dwelling salmonids, whether the space is defended or not.

An index of habitat saturation (PHS), which was developed from the territory–size regression, was able to predict the occurrence of density dependent growth, mortality, or emigration in 81% of the cases. The predictive power of the territory–size regression and PHS was surprisingly strong because both assume that space is the only factor influencing density; we deliberately ignored other important factors like habitat productivity and predation. The territory–size regression and PHS should be valuable tools for predicting maximum population densities, the occurrence of density-dependent population responses, and stocking densities of stream-dwelling salmonids.

Acknowledgments

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Large-Lake Responses to Declines in the Abundance of a Major Fish Planktivore — the Lake Michigan Example[1]

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Alewife abundances declined dramatically in southeastern Lake Michigan over 1973–77, several years before the lakewide decline occurred. The regional effects of this decline on adult copepod abundances, zooplankton biomass, and water clarity are examined. In the offshore region, the two largest copepods, *Limnocalanus macrurus* and *Diaptomus sicilis*, increased in abundance during the mid-1970's, reflecting the decrease in alewife predation. *Limnocalanus macrurus* abundances declined in later years, reflecting increased predation pressures from the increasing bloater population. The small-bodied *D. minutus* and the medium-bodied *D. ashlandi* exhibited no apparent response to the decline in alewife abundance. Large-bodied *D. oregonensis* and small-bodied *C. bicuspidatus thomasi* declined in abundance. Size-selective fish predation pressures continued to remain high in the inshore region: increased abundances of yellow perch and rainbow smelt apparently compensated for the alewife decline. Zooplankton biomass, zooplankton mean dry weight, and water clarity apparently were not affected by the decline in alewife abundance in either the inshore or offshore region. The results of this study are evaluated in terms of the lakewide decline in alewife abundance, the summer 1983 dominance of *Daphnia pulicaria* in offshore waters, the 1983 marked improvement in offshore water clarity, and later changes in summer offshore *D. pulicaria* populations.

L'abondance du gaspareau a diminué sensiblement dans le sud-ouest du lac Michigan au cours de la période de 1973 à 1977, plusieurs années avant que se produise la baisse à l'échelle du lac. Les effets régionaux de cette baisse sur l'abondance des copépodes adultes, la biomasse du zooplancton et la clarté de l'eau sont étudiées. Dans la région du large, l'abondance des deux plus gros copépodes, *Limnocalanus macrurus* et *Diaptomus sicilis*, a augmenté vers le milieu des années 1970, ce qui montre la baisse de prédation par le gaspareau. L'abondance de *L. macrurus* a diminué au cours des dernières années, ce qui traduit des pressions de prédation accrues de la population grandissante de Cisco de fumage. Aucune réaction apparente n'a été enregistrée par les organismes de petite taille *D. minutus* et de taille moyenne *D. ashlandi* face à la baisse de l'abondance du gaspareau. L'abondance des organismes de grande taille *D. oregonensis* et de petite taille *C. bicuspidatus thomasi* a diminué. Les pressions de prédation des poissons en fonction de la taille sont demeurées fortes dans la région côtière : il semble que l'abondance accrue de perchaudes et d'éperlans ait compensé la baisse du nombre de gaspareau. Apparemment, la biomasse du zooplanton, le poids moyen du zooplancton et la clarté de l'eau n'ont pas été modifiés par la diminution du nombre de gaspareau dans la région côtière ou du large. Les résultats de la présente étude sont évalués en fonction de la baisse de l'abondance du gaspareau à l'échelle du lac, de la dominance au cours de l'été de 1983 de *Daphnia pulicaria* dans les eaux du large, de l'amélioration marquée en 1983 de la clarté de l'eau du large, et des changements récents des populations pélagiques de *D. pulicaria* en été.

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Much of our understanding of factors affecting zooplankton community structure has been obtained from studies conducted in relatively small (<1 km^2), shallow (mean depth <10 m) water bodies. Among these classic studies were those that showed fish planktivores selectively consume the largest components of zooplankton communities resulting in a shift in community structure toward dominance by small taxa (Brooks and Dodson 1965; Galbraith 1967; Stenson 1972). Such effects may be reversible (Warshaw 1972).

The role of fish predation in shaping zooplankton community structure recently has gained new attention because of its potential implication for managing algal standing stocks (Carpenter et al. 1985). Large-bodied zooplankton grazers (especially *Daphnia*) tend to have higher grazing rates than small-bodied zooplankton (Haney 1973). Thus, it is theoretically possible to control algal standing stocks from above, i.e. by managing fish populations to produce a zooplankton community dominated by large-bodied zooplankton. This potential for control has been shown experimentally in a number of small, shallow waterbodies (Lynch and Shapiro 1981; Shapiro and Wright 1984; Spencer and King 1984). The potential for top-down management of larger, more complex systems is less well understood. Here I explore this issue by examining the co-occurring changes

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in alewife (*Alosa pseudoharengus*) and adult copepod abundances in southeastern Lake Michigan. Earlier, I examined the response of the *Daphnia* species assemblage to declines in alewife abundance (Evans and Jude 1986).

Lake Michigan: Background Information and Hypotheses

Lake Michigan, by nature of its large size (area = 57 850 km^2, mean depth = 99 m, maximum depth = 265 m), differs substantially from the small lakes and ponds in which most ecosystem manipulation studies have been conducted. The large horizontal and vertical scales of this Great Lake allow for a greater diversity of species. For example, Lake Michigan contains four species of *Diaptomus* while most lakes typically contain only one to three species (Rigler and Langford 1967; Roff et al. 1981). Inshore–offshore differences in zooplankton community structure develop and weaken seasonally (Evans et al. 1980). Such differences are most pronounced during thermal stratification when the inshore region serves as an important nursery area for alewife, yellow perch (*Perca flavescens*), and rainbow smelt (*Osmerus mordax*).

Historically, Lake Michigan supported a multiple species complex of planktivores and macrobenthic feeders including emerald shiners (*Notropis atherinoides*), yellow perch, and several species within the Coregonidae, e.g. lake whitefish (*Coregonus clupeaformis*), lake herring (*C. artedii*), and bloater (*C. hoyi*). Each species occupied specific depth regions of the lake (Wells and Mclain 1972). Overfishing and the sea lamprey invasion reduced the abundance of fish predators such as lake trout (*Salvelinus namaycush*) and burbot (*Lota lota*). This apparently allowed alewife and rainbow smelt to become established in Lake Michigan where they proliferated and eventually displaced several indigenous fish from their niches. Many species became extinct and food web dynamics were altered (Christie 1974).

More recently, alewife abundances declined markedly in Lake Michigan, possibly due to an aggressive salmonid stocking program and/or to several recent cold winters (Stewart et al. 1981; Jude and Tesar 1985; Eck and Wells 1987). During this period of declining alewife populations, large-bodied *Daphnia* increased in abundance in the offshore region: maximum water clarity also increased (Scavia et al. 1986; Evans and Jude 1986). These changes have spurred renewed speculation that an alternative (or additional) method for improving water clarity and controlling algal abundance in Lake Michigan and other Great Lakes could be based on top-down, management strategies (Kitchell et al. 1988): the more traditionally-employed, bottom-up strategies are based on phosphorus control.

Here, I continue to explore the changes which occurred in Lake Michigan zooplankton community structure, biomass, and water clarity during this period of declining alewife abundance: I place particular emphasis on the changes which occurred in the adult copepod species assemblage. This paper focuses on southeastern Lake Michigan where an exceptionally comprehensive monitoring study was conducted in the vicinity of the Donald C. Cook nuclear power plant: zooplankton studies reported here were conducted from April 1972 to May 1982 while fish studies were conducted from April 1973 to November 1982.

In southeastern Lake Michigan, alewife declined markedly in abundance over 1973–77 with abundances levelling off in later years: the mean annual catch for 1977–82 was approximately 25% that of the 1973–76 period (Fig. 1; Jude and Tesar 1985). In contrast, the lakewide decline in alewife abundance did not become pronounced until 1983 (Fig. 1; Eck and Wells 1987). Yellow perch (which inhabits the inshore) and bloater

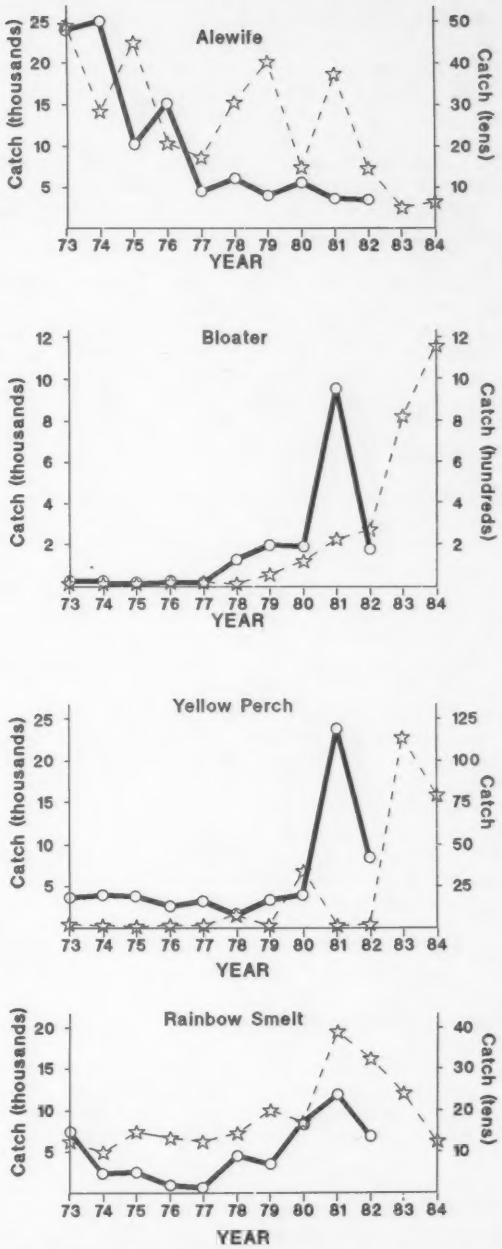


FIG. 1. Long-term April–October abundance trends (solid line) for forage fish in southeastern Lake Michigan, 1973–82. Redrawn from Jude and Tesar (1985). Catch is of >age 1 fish, except alewife, where catch is of >age 2 fish. Also shown (dotted line) are the lake-wide autumn abundance trends, 1973–84. Redrawn from Eck and Wells (1987). Catch is of >age 1 fish, except yellow perch, where catch is young-of-the-year.

(which inhabits offshore hypolimnetic waters) increased in abundance with the alewife population decline (Fig. 1). Therefore, the southeastern Lake Michigan monitoring study provides a unique opportunity to investigate the regional effects of a major decline in alewife abundance on zooplankton community structure, zooplankton biomass, and water clarity.

After evaluating the changes which occurred in zooplankton community structure, biomass, and water clarity in southeastern Lake Michigan over 1972–82, I review the changes which occurred in the offshore zooplankton community and the associated changes in water clarity over summer 1983–87. Of particular relevance, are the changes in the *Daphnia* assemblage. Finally, based on the new understandings gained from my own research in southeastern Lake Michigan and later research in the region offshore Grand Haven, I re-examine the hypothesis that top-down control strategies may be a useful management tool for controlling algal populations in large lakes.

Materials and Methods

The Lake Michigan copepod community is dominated by six species of copepods which vary substantially in size and life history. In decreasing order of mean body size, these are *Limnocalanus macrurus, Diaptomus sicilis, D. oregonensis, D. ashlandi, D. minutus,* and *Cyclops bicuspidatus thomasi* (Hawkins and Evans 1979). *Limnocalanus macrurus* is univoltine, reproducing in early winter: adults appear in summer. All four diaptomid species are bivoltine, reproducing in late winter-early spring and in mid-summer: they overwinter as adults. *Cyclops bicuspidatus thomasi* overwinters primarily in the immature copepodite stages, reaching adulthood by early spring, at which time it reproduces. Second and third reproductive pulses occur in midsummer and in late summer–early autumn (Torke 1975). During thermal stratification, *L. macrurus* inhabits the hypolimnion, *D. ashlandi* the upper metalimnion–lower epilimnion, *C. bicuspidatus thomasi* the lower epilimnion, while *D. minutus* and *D. oregonensis* are more strongly epilimnetic (Wells 1960; M. S. Evans, unpubl. data). Although Wells (1960) reported *D. sicilis* as preferring the upper layers, others (Wilson and Roff 1973; M. S. Evans, unpubl. data) have found it preferring hypolimnetic waters.

Zooplankton Sampling Methods

Lake surveys, the major component of the zooplankton monitoring studies, were conducted once a month, April through November. Data collected from April 1972 to May 1982 are used in this paper. While survey cruises were conducted in earlier years (1969, 1970, and 1971), a coarser plankton net was used than in later years; consequently, data collected during 1969, 1970, and 1971 are not used in this paper.

Lake survey data collected during spring (April, May), summer (July, August), and autumn (October) form the focus of this paper. Rough lake conditions in several years prevented November cruises from being conducted. Long-term trends in autumn copepod populations are based only on October data.

During each cruise, zooplankton were collected at a 14 (May, August) or 30 (April, July, October) station grid extending 11 km north and south and from 0.6 to 11 km offshore of the power plant. Station depths generally ranged from 4- to 45-m. In previous studies (Evans et al. 1980, 1982), the survey grid was divided into four depth-related regions. Here, long-term trends in spring, summer, and autumn zooplankton populations are discussed in the inshore (4- to 10-m depth contours) and offshore (30- to 45-m depth contours) regions. Depending on the cruise, seven (May, August) to 13 (April, July) stations were sampled in the inshore region and one (May, August) to three (April, July, October) in the offshore region during most cruises. In some Octobers, rough lake conditions prevented sampling in the 30- to 45-m depth region. In such instances (1975, 1976), data collected from the 20- to 30-m depth contour region were used to provide information on zooplankton abundances in the offshore region. Additional information on the history of the monitoring study is provided in Evans et al. (1985).

A 50-cm diameter, 156-μm mesh net equipped with a calibrated flowmeter was used to collect zooplankton. Replicate hauls were made at each station from approximately 1 m off the bottom to the surface. Surface-water temperature was measured at all stations and temperature–depth profiles at most stations. Secchi disk depth was measured with a 20.3-cm diameter white disk.

Beginning in January 1975, zooplankton were collected monthly (January–December) from the intake waters of the power plant. Intake sampling has been shown to provide representative estimates of zooplankton population trends in the inshore region (Evans and Flath 1984). Data collected during early winter (December–January) and late winter (February–March) are used to investigate long-term trends in overwintering copepod abundances. Early-winter data for 1975 are based on January collections only. Two replicate 5-min intake samples (approximately 1 m^3 each) were collected at sunset, midnight, sunrise, and noon from the intake forebay of the power plant. A Hale 30LC-1750 diaphragm pump withdrew water from the forebay and discharged it into a 20-cm diameter (February 1975–July 1977) or 30-cm (after July 1977), 156-μm mesh net suspended in a barrel of water.

Laboratory Methods

In the laboratory, zooplankton samples were divided in a Folsom plankton splitter to give two subsamples of approximately 300–600 organisms each. Adult copepods and cladocerans were identified to species while immature copepodites were identified to genus. Nauplii were enumerated but were not identified. Prior to 1974, zooplankton were identified to species only at a subset of stations sampled during the survey cruises.

Beginning in summer 1975, the mean dry weights of the numerically dominant taxa were determined for each sampling period. Total zooplankton biomass at each station was calculated from estimates of individual zooplankton dry weights and abundances (Hawkins and Evans 1979). Since zooplankton dry weights were not determined prior to 1975, average (1975–82) species dry weights were determined by month and these estimates were then used in calculating zooplankton biomass for earlier periods.

Data Presentation

Data are graphed, by species (Fig. 3–8), as mean spring (April–May), summer (July–August), and autumn (October) abundances by depth zone. For spring and summer graphs, the range in values (i.e. the April and May or the July and August cruise means) are shown. Intake data are presented for early winter (December–January means) and late winter (February–

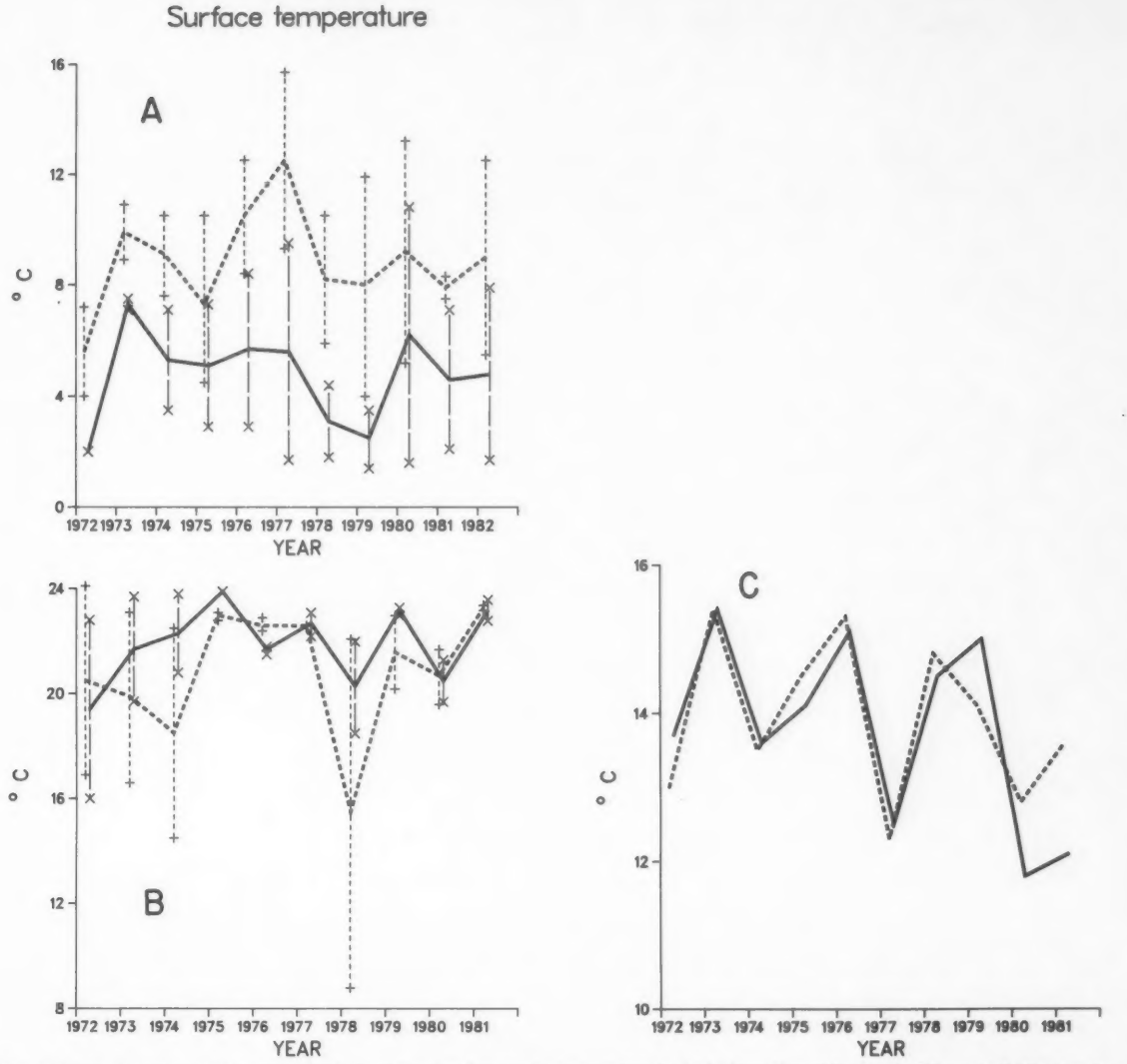


FIG. 2. Mean (A) spring, (B) summer, and (C) autumn surface-water temperatures in the inshore (dotted line) and offshore (solid line) regions of southeastern Lake Michigan. Vertical lines connect means of the two appropriate months.

March means); the range in monthly mean estimates also is shown. A similar approach was used in the presentation of water temperature, biomass, and water clarity data (Fig. 2, 9, 10).

Results

Thermal Regime

Surface-water temperatures were low during spring, high in summer, and moderate during autumn (Fig. 2). Inshore-offshore thermal gradients were strong during spring, a period of isothermal conditions. Thermal stratification was strong in summer. Relatively low surface-water temperatures in the inshore region generally were associated with upwellings. With the autumn erosion of the thermocline, the water column was often isothermal to depths of 20–30 m: inshore-offshore thermal gradients were weak (Evans et al. 1985). There was a weak trend for autumn surface-water temperatures to decline over 1972–1981.

General Features of Copepod Distributions, April 1972–May 1982

The most striking feature of copepod distribution patterns over spring through autumn (Figs. 3–8) was the pronounced tendency for adults to occur in lower abundances in the inshore rather than offshore region. The greatest differences in abundance were observed for the largest copepods, i.e. *L. macrurus*, *D. sicilis*, and *D. oregonensis*. Inshore-offshore differences in abundance were less pronounced for the smaller *D. ashlandi* and *C. bicuspidatus thomasi* and were weakest for *D. minutus*, the smallest calanoid copepod. Although water column depth

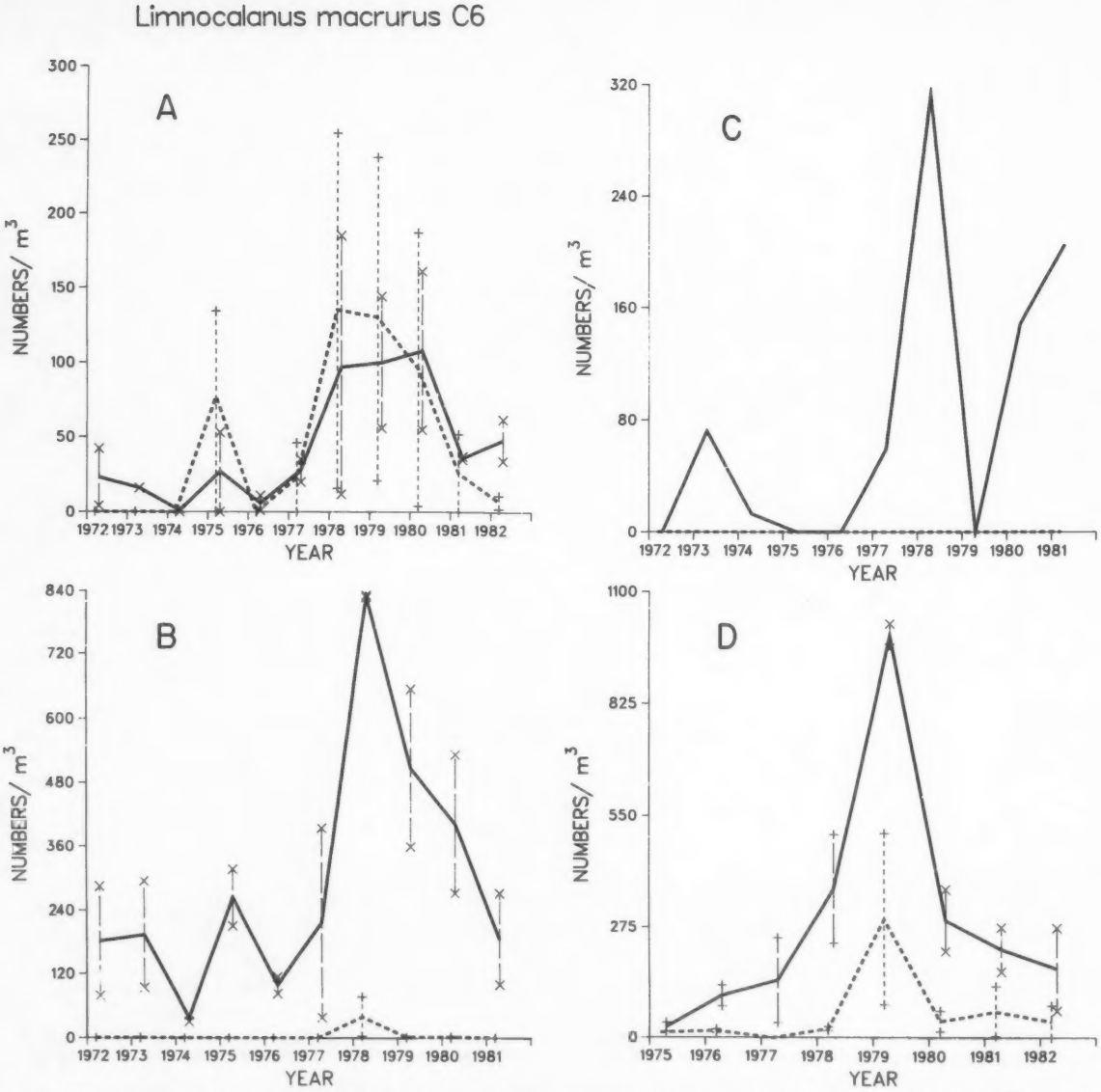


FIG. 3. Mean (A) spring, (B) summer, and (C) autumn *Limnocalanus macrurus* adult abundances in the inshore (dotted line) and offshore (solid line) regions of southeastern Lake Michigan. Also shown are mean abundances in (B) intake waters during early winter (dotted line) and late winter (solid line). Vertical lines connect means of the two appropriate months.

may have been an important factor limiting the abundance of hypolimnetic taxa such as *L. macrurus* and *D. sicilis* in the inshore region, factors related to zooplankton body size also must have been important. Inshore-offshore differences in abundance were much steeper for large-bodied epilimnetic taxa such as *D. oregonensis* and *Daphnia* spp. (Evans and Jude 1986) than for small-bodied epilimnetic taxa such as *D. minutus*.

Adult copepods increased markedly in abundance in the inshore region between autumn and early winter (Fig. 3–8). Part of this increase was due to the maturation of the autumn generation of immature *Cyclops* spp. and *Diaptomus* spp. copepodites to adults. Moreover, univoltine *L. macrurus* adults, which attain their maximum abundance in the offshore region during summer, also increased in abundance in intake waters through autumn and early winter, highest densities were attained in late winter. These increased abundances reflect the consequences of physical transport of water (and zooplankton) from the offshore and the relatively high survival of adults in the inshore region during the cooler seasons of the year.

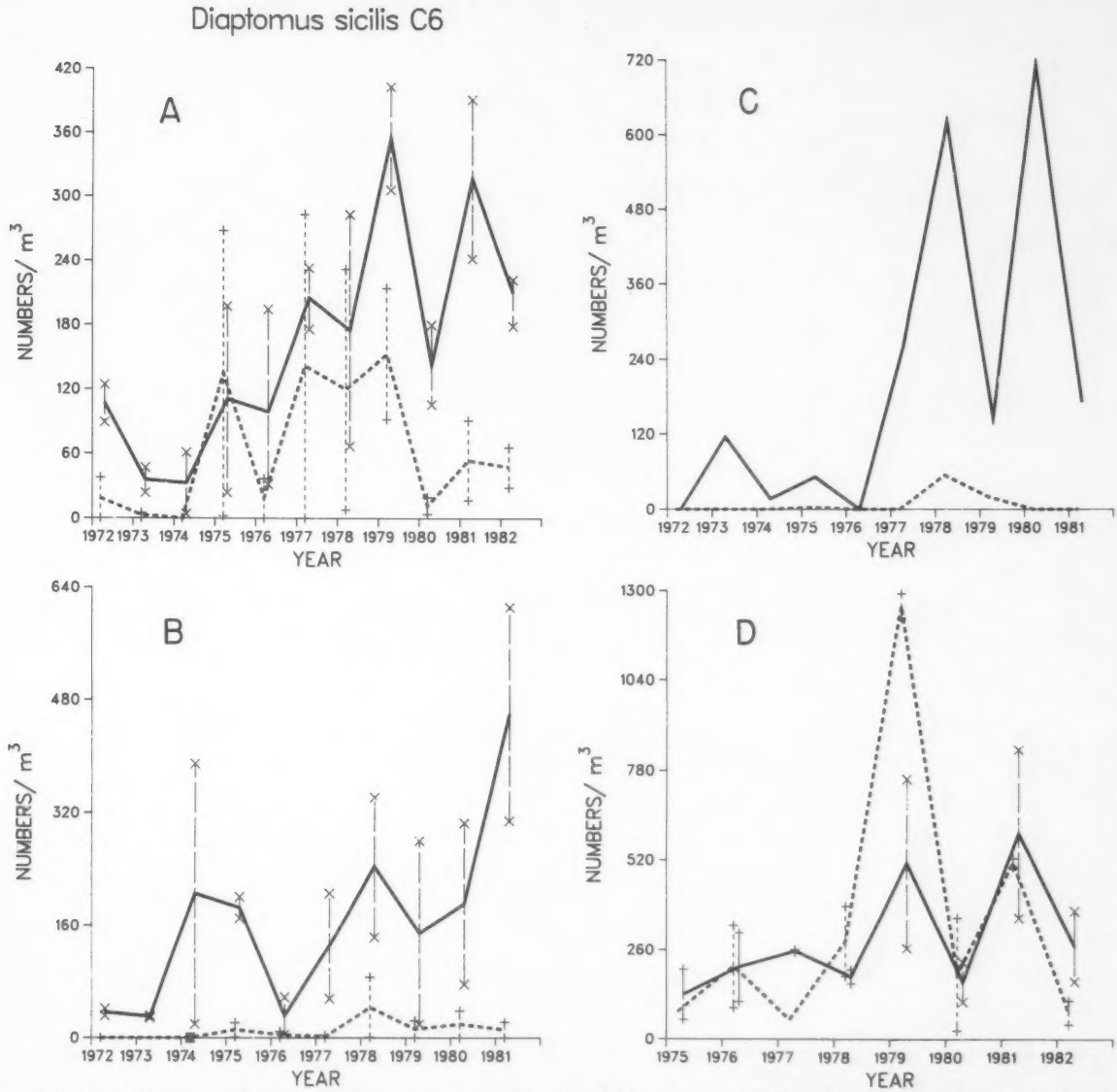


FIG. 4. Mean (A) spring, (B) summer, and (C) autumn *Diaptomus sicilis* adult abundances in the inshore (dotted line) and offshore (solid line) regions of southeastern Lake Michigan. Also shown are mean abundances in (B) intake waters during early winter (dotted line) and late winter (solid line). Vertical lines connect means of the two appropriate months.

Long-Term Trends in Adult Copepod Abundances

Limnocalanus macrurus and Diaptomus sicilis: the offshore

Adult *L. macrurus* abundances (Fig. 3) were low during the early 1970's, a period of declining alewife abundance. Adults increased in abundance in the late 1970's, with abundances declining in later years. Relatively low *L. macrurus* abundances in autumn 1979 may have been associated with moderately high temperatures (13°C; Evans et al. 1985) in the deeper regions of the water column. In contrast, vertical mixing was less intense in autumn 1978, a year of similarly high surface-water temperatures (Evans et al. 1982). Adult *D. sicilis* exhibited similar long-term abundance trends (Fig. 4) in offshore waters as *L. macrurus*, i.e. low abundances in the early 1970's and increased abundances in the late 1970s. In contrast to *L. macrurus*, abundances of adult *D. sicilis* did not decline during the early 1980's.

Limnocalanus macrurus and Diaptomus sicilis: the inshore

During spring, adult *L. macrurus* and *D. sicilis* abundances increased (Fig. 3, 4) during the mid-1970's and then declined during the late 1970's and early 1980's. Inshore-offshore abundance differences for *D. sicilis* diminished during the mid-1970's but intensified over the late 1970's and early 1980's. Abundances of both species remained low over summer and autumn 1972–81. Winter populations of *L. macrurus* and

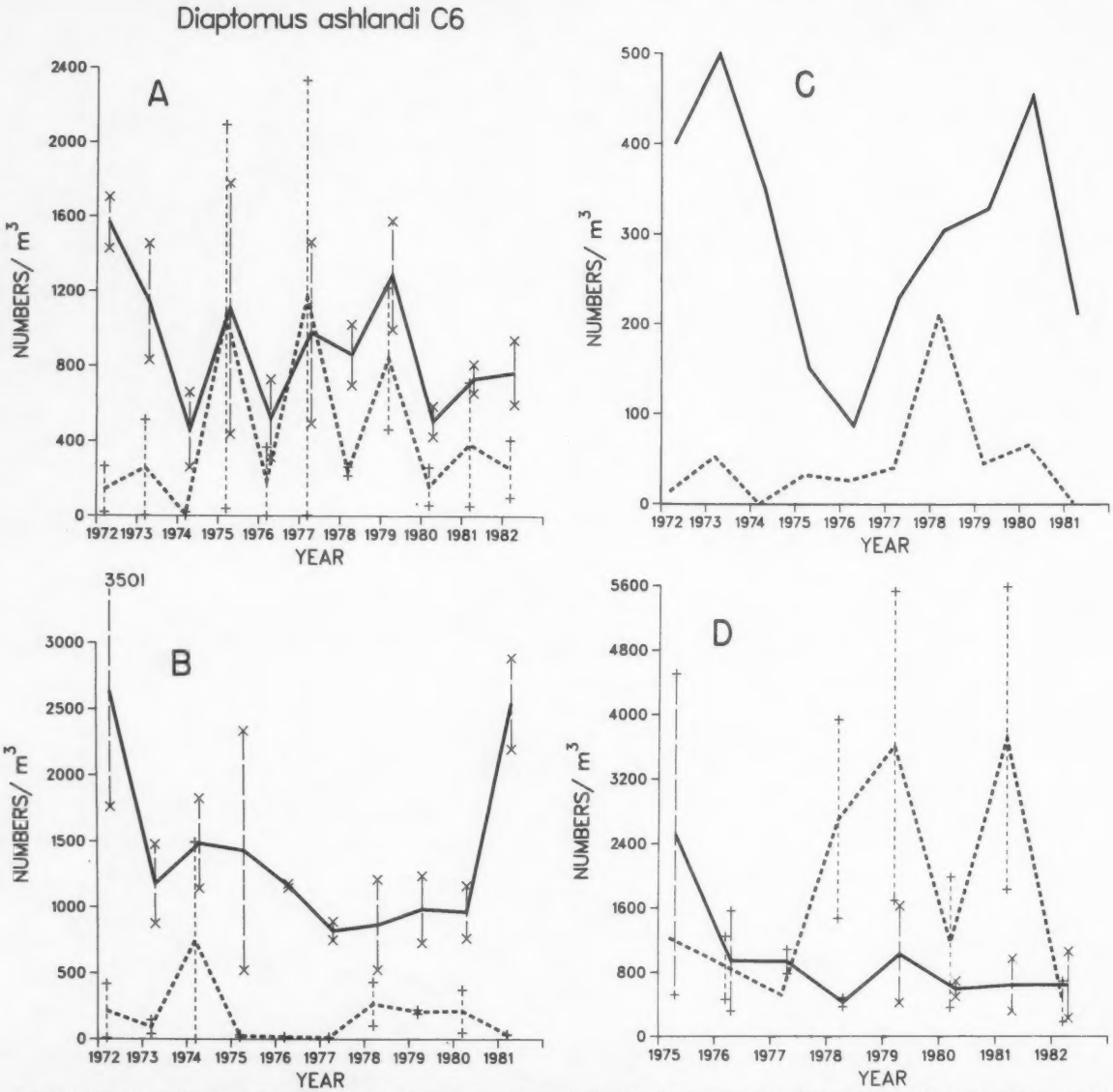


FIG. 5. Mean (A) spring, (B) summer, and (C) autumn *Diaptomus ashlandi* adult abundances in the inshore (dotted line) and offshore (solid line) regions of southeastern Lake Michigan. Also shown are mean abundances in (D) intake waters during early winter (dotted line) and late winter (solid line). Vertical lines connect means of the appropriate months.

D. sicilis exhibited a similar long-term trend as was observed in the offshore region during spring and summer, i.e. increasing abundance in the late 1970's followed by a decline (*L. macrurus*) or levelling off (*D. sicilis*) in later years.

Diaptomus ashlandi and D. minutus

There were only small changes in long-term abundance patterns of *D. ashlandi* and *D. minutus* (Fig. 5, 6). In the offshore region during spring, *D. minutus* densities were greater in the early 1970's than in later years. During autumn in the offshore region, there was an inverse relationship in long-term abundance patterns of *D. ashlandi* and *D. minutus*.

In the inshore region during spring, *D. ashlandi* densities were exceedingly low during the early 1970's, higher in the mid-1970's, and then low again in later years.

Cyclops bicuspidatus thomasi and D. oregonensis: the offshore

Long-term abundance trends for *C. bicuspidatus thomasi* and *D. oregonensis* were complex. Adult *C. bicuspidatus thomasi* exhibited a trend of declining abundance over spring 1972–82 (Fig. 7). Abundances were higher in summer 1972 than in later summers, abundances changed little over summer 1973–81. *Cyclops bicuspidatus thomasi* densities generally declined over

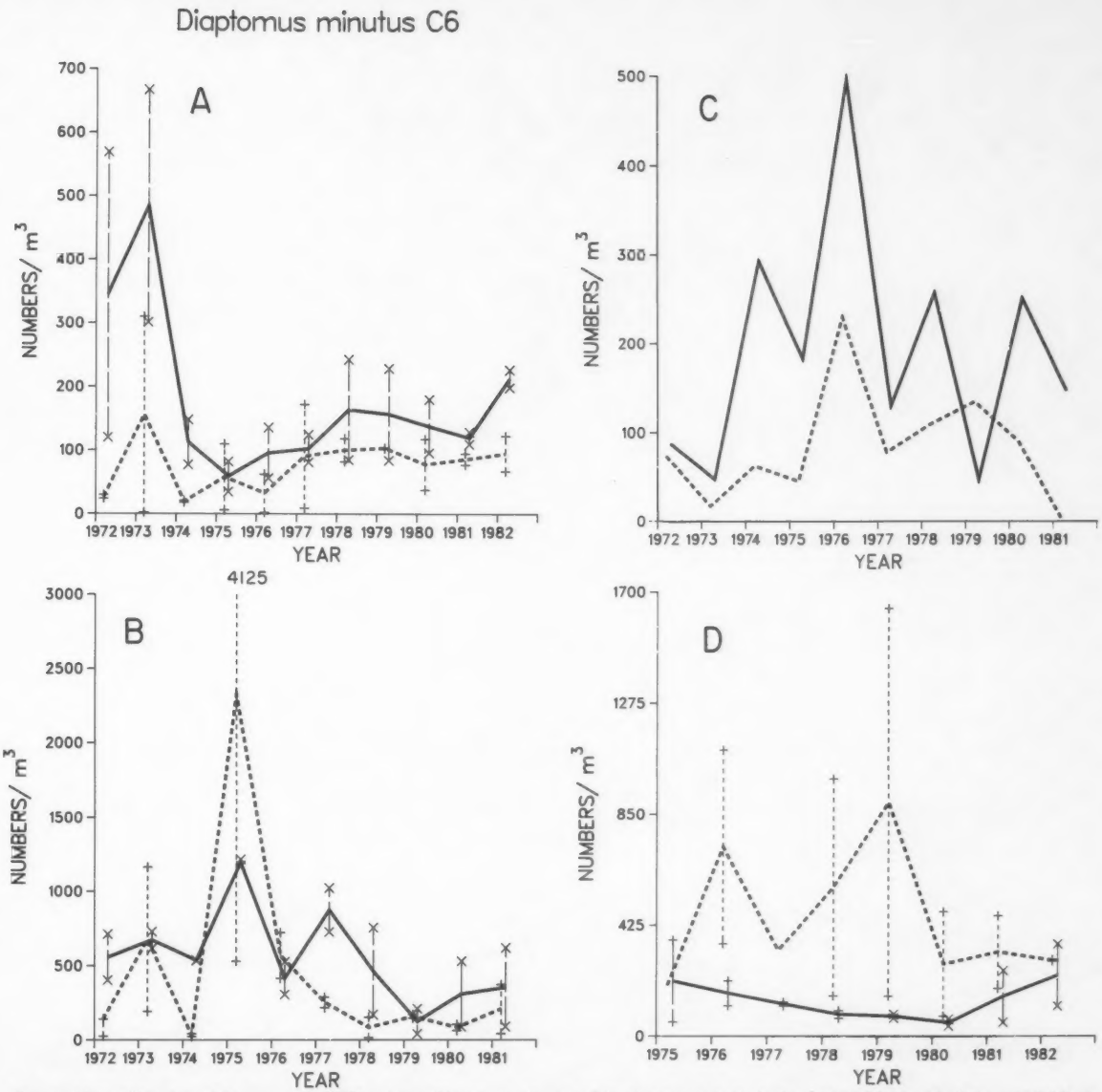


FIG. 6. Mean (A) spring, (B) summer, and (C) autumn *Diaptomus minutus* adult abundances in the inshore (dotted line) and offshore (solid line) regions of southeastern Lake Michigan. Also shown are mean abundances in (D) intake waters during early winter (dotted line) and late winter (solid line). Vertical lines connect means of the two appropriate months.

autumn 1972–81: this trend was strongly reversed in 1979 and 1980.

Adult *D. oregonensis* exhibited a trend of declining abundance over spring 1972–82 (Fig. 8). During summer, *D. oregonensis* abundances increased until 1977; after that, abundances declined. Autumn densities changed little over 1972–81.

Cyclops bicuspidatus thomasi and D. oregonensis: the inshore

During spring, *C. bicuspidatus thomasi* and *D. oregonensis* abundances (Figs. 7, 8) were low in the early 1970's, increased in the mid-1970's, and then declined in later years. Neither species exhibited any long-term change in abundance during summer or autumn. Overwintering populations of *C. bicuspidatus thomasi* and *D. oregonensis* exhibited a late-winter trend of declining abundance which was similar to that observed in spring in the offshore.

Long-Term Trends in Total Zooplankton Biomass

In general, the inshore region was dominated by smaller zooplankton than the offshore region; mean dry weight of an individual zooplankton generally was less in the inshore than offshore region (Fig. 9). There was no obvious trend in mean

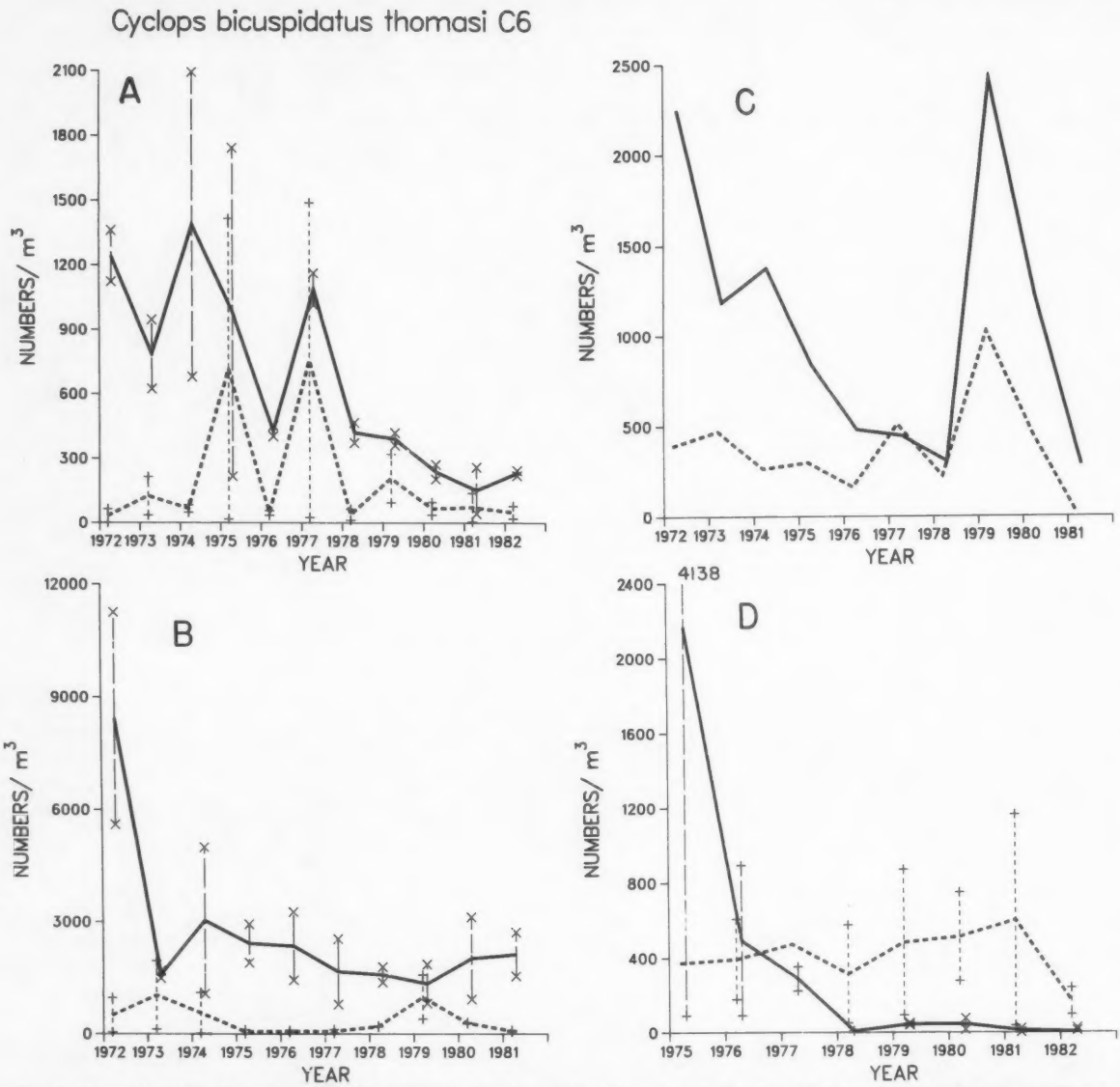


FIG. 7. Mean (A) spring, (B) summer, and (C) autumn *Cyclops bicuspidatus thomasi* adult abundance in the inshore (dotted line) and offshore (solid line) regions of southeastern Lake Michigan. Also shown are mean abundances in (D) intake waters during early winter (dotted line) and late winter (solid line). Vertical lines connect means of the two appropriate months.

zooplankton dry weight in the inshore region over the study period.

Similarly, there were no obvious long-term trends in mean zooplankton dry weight in the offshore region over spring 1972–82 and summer and autumn 1972–77. Zooplankton mean dry weight did increase markedly in summer and autumn 1978 but declined in later years to values slightly higher than (summer) or approximately equal (autumn) to values observed over 1972–77.

In general zooplankton biomass (mg/m^3) was substantially greater in the offshore than inshore region (Fig. 9): this was due to zooplankton being more abundant and, on average, heavier in offshore than inshore waters. Zooplankton biomass was low in spring, increased in summer, and declined somewhat in autumn.

There were no pronounced, long-term changes in total zooplankton biomass in the offshore region over the study period (Fig. 9). Total biomass, however, was relatively high in summer 1978 and autumn 1980 when compared to earlier and later years. Similarly, no obvious trends were noted in inshore region zooplankton biomass during summer and autumn 1972–81. However, during spring, zooplankton biomass increased in the

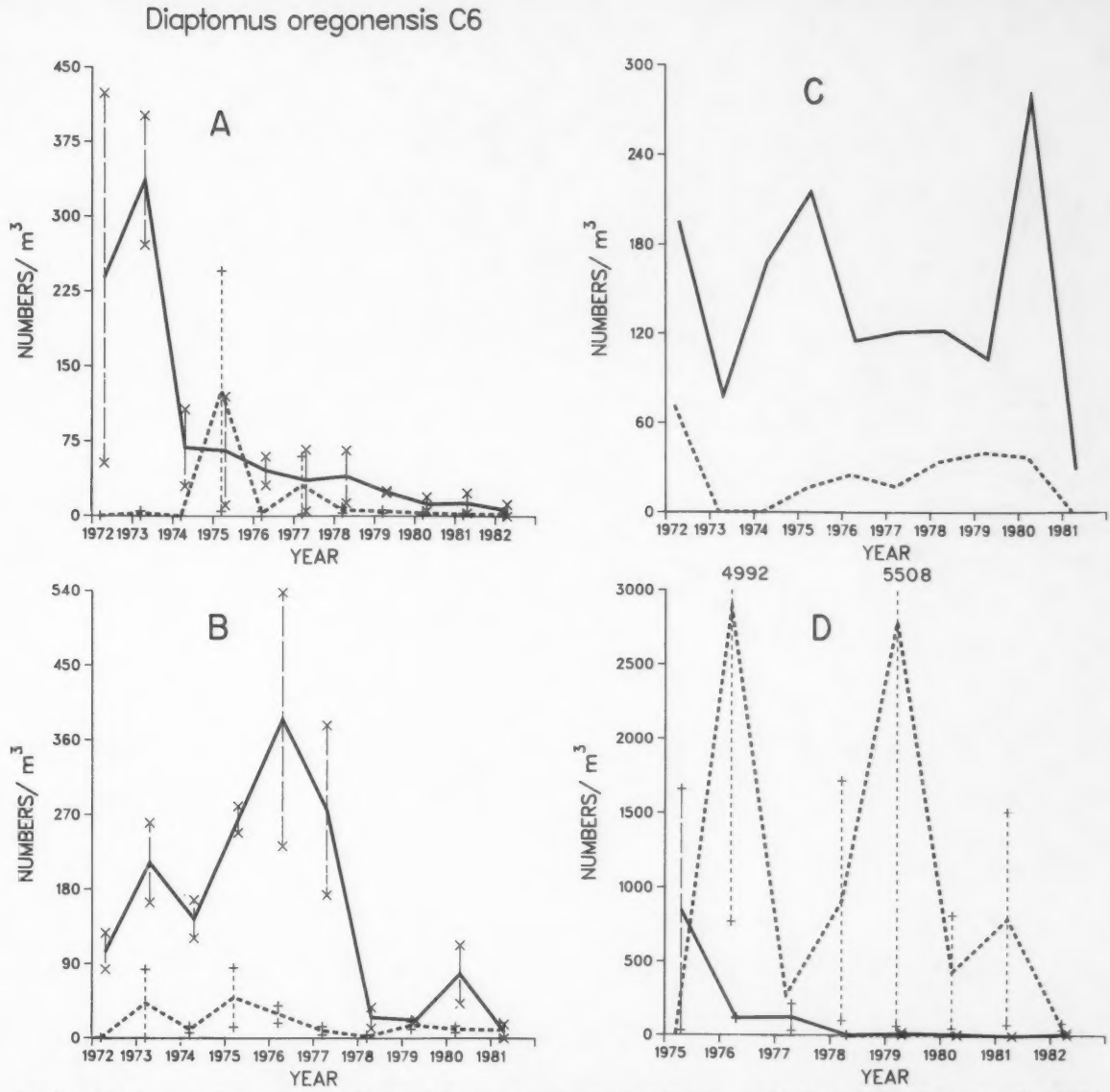


FIG. 8. Mean (A) spring, (B) summer, and (C) autumn *Diaptomus oregonensis* adult abundances in the inshore (dotted line) and offshore (solid line) regions of southeastern Lake Michigan. Also shown are mean abundances in (D) intake waters during early winter (dotted line) and late winter (solid line). Vertical lines connect means of the two appropriate months.

inshore region from very low values in the early 1970's, to peak values in the mid-1970's, and then declined somewhat in later years.

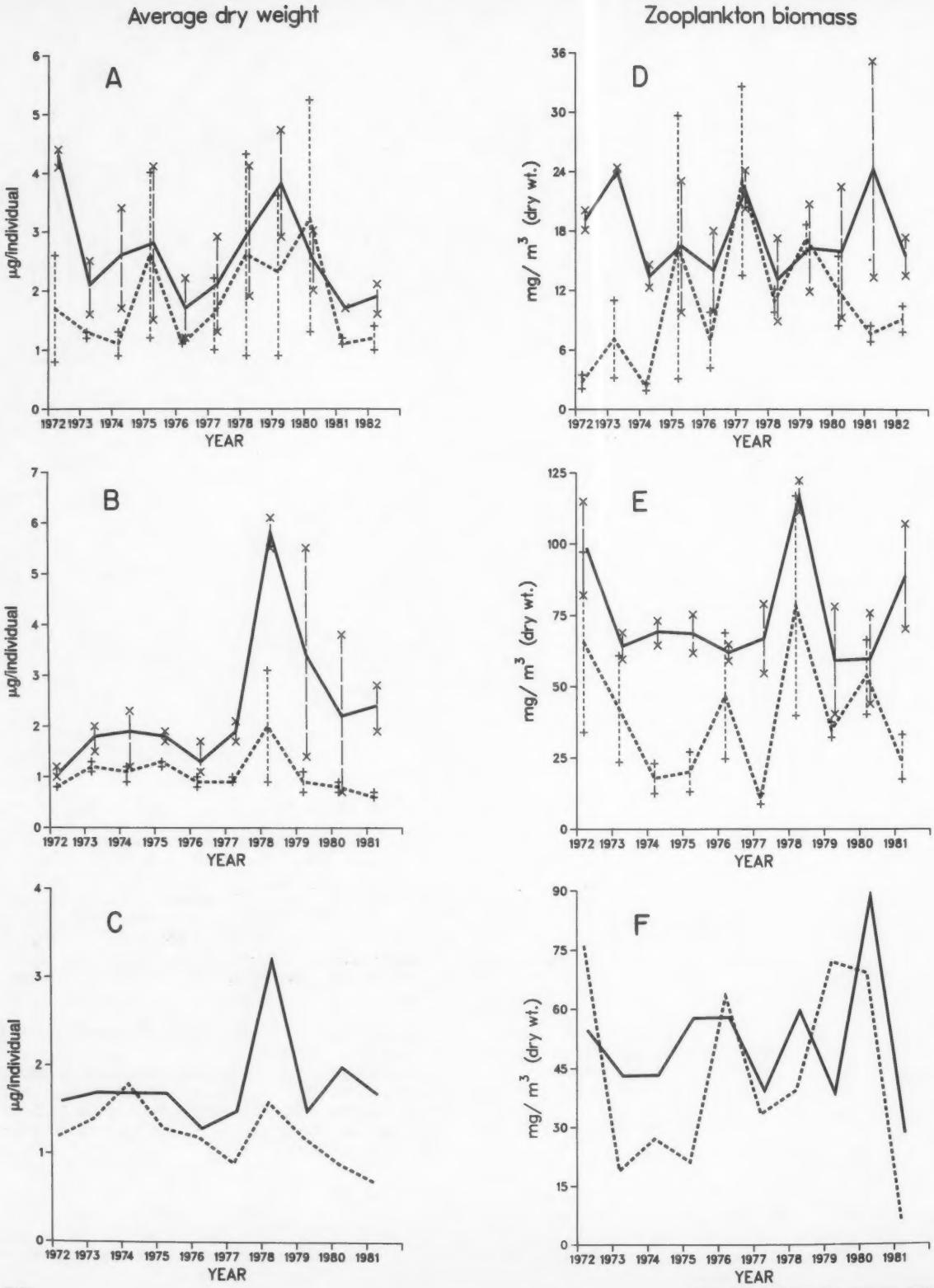
Long-Term Trends in Water Clarity (Secchi Disc Depth)

Water clarity was relatively low in inshore waters from spring to autumn (Fig. 10). Offshore water clarity was higher, increasing from spring to summer, and then declining somewhat in autumn. There were no pronounced long-term trends in water clarity over spring 1972–82 and autumn 1972–81 in the offshore region. However, water clarity was markedly higher in the offshore region during summer 1977–79 than in earlier and later years.

If summer 1978, data are excluded (because of the strong upwelling events; Fig. 2B), there was a weak trend for water clarity to increase in the inshore region over summer 1972–81. There was even weaker evidence of such a trend over spring 1972–82 and autumn 1972–81.

Discussion

In Lake Michigan, zooplankton community structure and standing stocks vary with distance from shore. These differ-


Average dry weight
Zooplankton biomass
A
B
C
D
E
F
µg/individual
mg/ m³ (dry wt.)
YEAR
1972 1973 1974 1975 1976 1977 1978 1979 1980 1981 1982

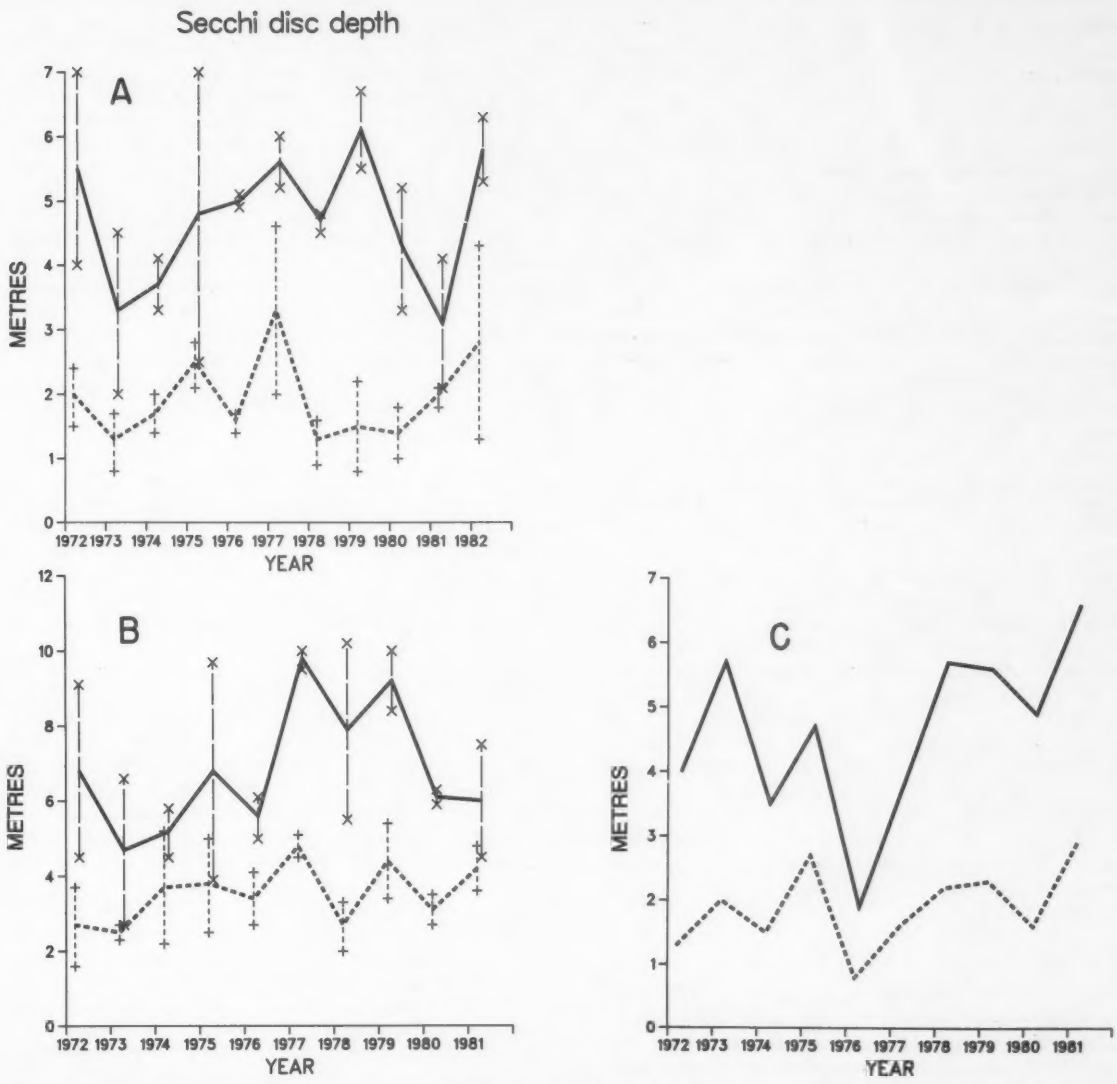


FIG. 10. Mean (A) spring, (B) summer, and (C) autumn Secchi disc depth in the inshore (dotted line) and offshore (solid line) regions of southeastern Lake Michigan. Vertical lines connect means of the two appropriate months.

ences develop in spring, intensify through summer, and weaken through late autumn (Evans and et al. 1980). Size-selective fish predation has been hypothesized as being one of the most important factors contributing to the formation of inshore-offshore differences in zooplankton community structure (Evans et al. 1980). Inshore-offshore variation in the intensity of size-selective feeding pressure appears to be intense, counteracting opposing forces such as the physical exchange of water (and zooplankton) between the inshore and offshore region.

During spring, alewife, yellow perch, and rainbow smelt migrate inshore to spawn; these fish are planktivorous as larvae and obligate or facultative planktivores as adults (Scott and Crossman 1973). Although alewife and smelt later migrate offshore, the inshore region continues to serve as an important nursery area for their larvae and yellow perch larvae through late spring to autumn (Wells 1968). Hence, most large-bodied zooplankton, including epilimnetic species such as *D. oregonensis* (Fig. 8) and *Daphnia* spp. (Evans and Jude 1986), are

FIG. 9. (*Continued*)
Mean (A) spring, (B) summer, (C) autumn average dry weight of zooplankton in the inshore (dotted line) and offshore (solid line) regions of southeastern Lake Michigan. Also shown are the mean (D) spring, (E) summer, and (F) autumn zooplankton biomass for the same time periods and locations. Vertical lines connect means of the two appropriate months.

relatively rare in the inshore region during these periods of intense, size-selective fish predation. Large-bodied zooplankton which are transported into the inshore from the offshore region (e.g. during upwellings and other exchanges) are rapidly consumed by the abundant population of size-selective planktivorous fish; this predation is most intense in summer.

During winter, the inshore region is relatively devoid of planktivorous fish: alewife, rainbow smelt, yellow perch, and bloater overwinter in deeper regions of the lake (Wells 1968). Consequently, fish predation on the inshore zooplankton community is least intense during winter: large-bodied zooplankton which are transported into the inshore region persist. This is evident from the fact that adult *L. macrurus* increased in abundance in intake waters from below detection limits in autumn to moderately high numbers in early winter to higher values in late winter; as a univoltine species, adult *L. macrurus* attain their maximum abundances in summer and in the offshore region (Fig. 3B). Similarly, *D. sicilis*, *D. ashlandi*, and *D. oregonensis* occurred in substantially higher numbers in the inshore region in early winter than during summer and autumn (Fig. 4, 5, 8). The weakest seasonal differences in abundance were exhibited by *D. minutus* (Fig. 6), the smallest calanoid copepod.

More recent observations, based on the response of the zooplankton community to changes in forage fish abundance, provide further support for the hypothesis that size-selective fish predation is an important factor affecting inshore-offshore differences in zooplankton community structure and biomass during the warmest seasons of the year. Compelling evidence comes from two earlier studies, one reporting changes in summer and autumn *Daphnia* spp. community structure in inshore and offshore waters over 1972–84 (Evans and Jude 1986) and the other reporting declines in zooplankton biomass in the inshore region over summer 1982–84 (Evans 1986). The present study examines the more subtle responses exhibited by adult copepods and total zooplankton biomass to declines in alewife abundance in inshore and offshore waters of southeastern Lake Michigan.

Adult Copepod Abundance Trends

Two species of adult copepods, *L. macrurus* and *D. sicilis*, responded in basically predictable ways to the long-term decline in alewife abundance and the subsequent increase in bloater, yellow perch, and rainbow smelt abundances. As a large-bodied copepod, *L. macrurus* and *D. sicilis* are especially vulnerable to size-selective fish predation, especially from hypolimnetic predators i.e. alewives and bloaters. *L. macrurus* and *D. sicilis* were scarce in the offshore region during the early 1970's when alewives were abundant. Both species increased in abundance when alewife populations declined during the mid- to late-1970's. *Limnocalanus macrurus* abundances declined in later years when bloater numbers increased while *D. sicilis* abundances remained unchanged. Because *D. sicilis* is smaller than *L. macrurus*, it may have experienced less predation pressure from bloaters. Similarly, long-term trends in adult *L. macrurus* and *D. sicilis* abundances in the inshore region during winter and spring (when substantial exchange of water occurs) were, in part, a reflection of events occurring in the offshore.

Adult *L. macrurus* continued to be excluded from the inshore region during summer and autumn over 1972–81 despite the long-term decline in alewife. Although temperature probably was the major factor excluding adult *L. macrurus* at these times, size-selective fish predation also must have been important. For example, despite the strong upwelling events of summer 1978 (Fig. 2b), *L. macrurus* abundances remained substantially lower in the inshore (Fig. 3b). Unlike *L. macrurus*, spring inshore-offshore differences in *D. sicilis* abundance decreased in the mid-1970's, possibly suggesting that this diaptomid experienced less size-selective predation pressure than *L. macrurus* during this period. However, inshore-offshore differences in *D. sicilis* abundances intensified in later years as rainbow smelt and yellow perch populations increased.

The medium-sized *D. ashlandi* and small-bodied *D. minutus* exhibited no obvious direct responses to the long-term decline in alewife abundance in the offshore region. The lack of response to the alewife decline suggests that alewife had a minor effect on *D. ashlandi* and *D. minutus* abundances during the 1970's; as metalimnetic/epilimnetic taxa, *D. minutus* and *D. ashlandi* should have been relatively immune to predation from adult bloaters. Alternatively, other factors (e.g. reduced food resources, increased competition) may have compensated for the reduction in alewife predation.

Similarly, reductions in alewife abundance had minor effects on adult *D. ashlandi* in the inshore region. Abundances of spring populations increased during the mid-1970's as alewife numbers declined and then increased as rainbow smelt and yellow perch numbers increased. No effects were noted for the adult *D. minutus* population.

The medium-bodied *D. oregonensis* and the small-bodied *C. bicuspidatus thomasi*, exhibited long-term abundance trends which are not readily explained in terms of direct fish-predation effects. In the offshore region, the summer cohort of *D. oregonensis* adults increased in abundance until 1977, suggesting a relaxation in alewife predation pressures, however, abundances decreased thereafter. As an epilimnetic copepod, *D. oregonensis* should have been relatively immune to predation pressures exerted by increased adult bloater populations; other factors must have limited the expected *D. oregonensis* population increase. Overwintering *D. oregonensis* adults exhibited a trend of declining abundance, this trend was even more evident for the spring offshore population. The causal factor(s) for this decline remains open to speculation. Similarly, the causal factor for the general long-term decline in adult *C. bicuspidatus thomasi* abundances (also an epilimnetic species) in late winter, spring, and summer offshore waters have no explanation in direct fish predation effects.

Water Clarity and Biomass Trends

Although alewife abundances declined markedly in southeastern Lake Michigan over 1973–82, total zooplankton biomass in the offshore region remained unchanged: increased abundances of some taxa (e.g. *D. sicilis*) were compensated for by decreased abundances of others (e.g. *D. oregonensis*). Similarly, total zooplankton mean dry weight did not change either in spring or autumn. The strong summer 1978 increase in mean dry weight and the subsequent decline in later years was associated primarily with increasing and decreasing abundances of *L. macrurus* copepods. Large-bodied immature *Diaptomus* spp. (probably *D. sicilis*) were also more abundant and *Daphnia* spp. heavier (Evans and Jude 1986) during the late 1970's and early 1980's than in earlier years.

During spring, reductions in alewife abundances apparently resulted in an increase in the mean size and total biomass of

zooplankton inhabiting the inshore region over the mid-1970's to late 1970's. Mean size and total biomass decreased in 1981 and 1982 as yellow perch and rainbow smelt abundances increased. However, zooplankton biomass and mean dry weight did not change substantially in the inshore region over summer and autumn 1972–81. This suggests that, during these seasons, size-selective fish predation pressures did not change. Reductions in alewife predation pressure apparently were compensated for by increased predation pressures from yellow perch and rainbow smelt, especially from young-of-the-year.

Despite the strong regional decline in alewife abundance, there was no marked improvement in water clarity in the inshore region over spring 1972–82 and autumn 1972–81. Although there was a weak trend for water clarity to increase in the inshore region over summer 1972–81, this increase cannot be related to direct top-down effects of reductions in alewife abundance: zooplankton total biomass and mean size did not exhibit a concurrent trend of increase. A more likely explanation is that increased water clarity was related to reductions in phosphorus loadings to Lake Michigan (Scavia et al. 1986).

Similarly, there was no obvious improvements in water clarity in the offshore region of Lake Michigan over spring 1972–82 and autumn 1972–81. However, water clarity was markedly higher during summer 1977–79 than in earlier and later years. Relatively high water clarity was also observed in the region offshore Grand Haven in summer 1977. This increase was related to the prolonged ice cover which occurred during winter 1976/1977, resulting in a reduction in sediment resuspension, spring total-phosphorus concentrations, and summer chlorophyll concentrations (Scavia et al. 1986); zooplankton mean size and total biomass were comparable to values observed in earlier years. The causal factor for the relatively high water clarity in summer 1978 is unknown; zooplankton mean size and total biomass were relatively high in 1978, possibly suggesting that top-down effects were important. However, large-bodied, epilimnetic *Daphnia* grazers were minor components of the zooplankton biomass at this time (Scavia et al. 1986). Moreover, although zooplankton biomass and mean size decreased in summer 1979 (with the decline in *L. macrurus* abundances), water clarity remained high. Overall, there is little conclusive evidence that top-down effects of reduced alewife abundances in southeastern Lake Michigan resulted in a pronounced and persistent improvement in water clarity.

Later Years

The lakewide decline in alewife abundances became strongly evident in 1983 and continued through 1984. Unfortunately, the monitoring study in southeastern Lake Michigan was formally completed in May 1982. Limited data were collected in the inshore region of southeastern Lake Michigan over summer 1982–84 (Evans and Jude 1986; Evans 1986) while offshore-region data were obtained at a 100 m station approximately 20 km off Grand Haven (Evans 1986; Scavia et al. 1986; Dorazio et al. 1987; Lehman 1988).

In the inshore region of southeastern Lake Michigan, yellow perch became especially abundant over summer 1982–84. Zooplankton abundance and biomass declined precipitously as an apparent consequence on intensified size-selective predation from yellow perch (Evans 1986). Despite this decline in zooplankton biomass, water clarity apparently remained high.

In the 100-m depth region offshore Grand Haven, the very large-bodied *Daphnia pulicaria*, which appeared sporadically in southeastern Lake Michigan over 1978–81, became a community dominant in 1982 (Evans and Jude 1986). In summer 1983, it accounted for the majority of the *Daphnia*-dominated (72%) zooplankton biomass. As a large-bodied cladoceran, *D. pulicaria* has a high grazing rate. Thus, zooplankton grazing rates, based on August experiments, were high averaging 7.09 mL/μg/d or, assuming a summer zooplankton biomass of 79 mg/m^3, 560 mL/m^3/d (Scavia et al. 1986). Thus, the zooplankton community required only 1.8 d to clear the epilimnion. In contrast, the phytoplankton turnover rate was 3 d. Moreover, epilimnetic chlorophyll concentrations were lower (ca. 0.5 μg/L) and Secchi disc depths (ca. 15 m) higher than in earlier years (Scavia et al. 1986). Strong improvements in summer 1983 water clarity were attributed to top-down effects, i.e. a major reduction in alewife which allowed large-bodied *Daphnia* grazers to predominate and to exert intense grazing pressure on the algae (Scavia et al. 1986).

This strong improvement in offshore water-clarity in summer 1983 stimulated much interest in the feasibility of using top-down management strategies for controlling epilimnetic phytoplankton populations in the Great Lakes (Kitchell et al. 1988). The potential, long-term practicality of this approach can be evaluated through the consideration of the changes which occurred in the offshore zooplankton community after summer 1983. Of particular relevance was the ability of *D. pulicaria* to continue dominating the zooplankton biomass.

Although total zooplankton biomass in the offshore region was similar in summer 1983 and 1984, *Daphnia* spp. biomass was approximately half as great in 1984 (ca. 29 mg/m^3) than in 1983 (ca. 57 mg/m^3). Similarly, epilimnetic chlorophyll concentrations were higher (ca. 1.1 μg/L) and water clarity lower (ca. 13 m vs. 15 m) in summer 1984 (Scavia et al. 1986). Thus, as a probable consequence of its lower biomass, *D. pulicaria* apparently was less effective in controlling epilimnetic phytoplankton abundances in summer 1984.

In summer 1985, *D. pulicaria* accounted for only 17% of the total epilimnetic zooplankton biomass (calculated from figure 3 in Dorazio et al. 1987) vs. 80% of the 0–40 m zooplankton herbivore biomass in 1983. Similarly, August weight-specific zooplankton grazing rates (<10 μm phytoplankton size cateogry) were lower in 1985 (1.15 mL/μg/d) than in 1983 (7.09 mL/μg/day). Assuming a summer 1983 zooplankton biomass of 36 mg/m^3 (calculated from figure 1 in Dorazio et al. 1987), the epilimnetic zooplankton community filtered 41.4 mL/m^3/d. Thus, epilimnetic zooplankton required 24.2 d to clear the epilimnion vs. an estimated 1.8 d in August 1983. Because August 1985 phytoplankton turnover rates were higher (6.9 d) than turnover rates based on grazing, zooplankton (including *D. pulicaria*) clearly were unable to control epilimnetic phytoplankton abundance increases (Dorazio et al. 1987).

According to Dorazio et al. (1987), *D. pulicaria* exerted relatively weak grazing pressures on the summer 1985 epilimnetic phytoplankton community because it inhabited the epilimnion only during nighttime hours. In contrast, *D. pulicaria* apparently was able to control epilimnetic phytoplankton abundance increases in summer 1983 because it maintained a more constant presence in the epilimnion (Dorazio et al. 1987). However, Schulze and Brooks (1987) indicated that, in August 1983, *D. pulicaria* was nearly twice as abundant in the 0–12 m depth strata at night (720/m^3) than during the day (335/m^3). Moreover, the *D. pulicaria* population was largely concentrated at the 12–22 m depth strata with abundances averaging 2800/m^3 during the day and 3040/m^3 at night.

Although *D. pulicaria* continued to persist in Lake Michigan in summer 1987, it was a minor component of the June–July zooplankton community accounting for less than 0.1% of the zooplankton (excluding nauplii) on a numerical basis (calculated from table 1 in Lehman 1988). Zooplankton density estimates are expressed as 0–95 m areal abundances and thus are not readily comparable to previous density estimates based on 0–40 m volumetric calculations of abundance (Evans and Jude 1986) and biomass (Scavia et al. 1986). In order to estimate summer 1987 *Daphnia* spp. volumetric abundances, mean July–August *Daphnia* spp. areal abundances were estimated based on data presented in table 3 (Lehman 1988). This mean value was then divided by 95 m and multiplied by a 1.6 correction factor (Evans and Jude 1986). Total *D. retrocurva*, *D. galeata mendotae*, and *D. pulicaria* abundances averaged 207/m^3 or some 10–50 times lower than that observed for *D. pulicaria* alone over summer 1983 (Lehman 1988; Evans and Jude 1986). Despite this reduced *D. pulicaria* abundance, summer epilimnetic chlorophyll concentrations were similar in 1983 and 1987. Lehman (1988) concluded that herbivory was not the major factor controlling surface (0–20 m) phytoplankton abundances in the offshore region over summer 1983–1987. Thus, the contributory role of *D. pulicaria* grazing to the increased water clarity and low epilimnetic chlorophyll concentrations of summer 1983 was questioned.

Thus, studies conducted subsequent to Scavia et al.'s (1986) investigation have shown that *D. pulicaria* was unable to dominate the zooplankton biomass in the offshore region as in summer 1983 (Dorazio et al. 1987; Lehman 1988; Scavia et al. 1986). This reduced dominance in later years (1984–87) could have been due to several factors. Foremost among these is increased predation pressures from alewife and bloaters. Alewife abundances, although exceedingly low in 1983 (Fig. 1), increased in later years: in 1987, alewife abundances exceeded those observed in 1977, 1978, and 1980 (G. W. Eck, U. S. Fish and Wildlife Service, Ann Arbor, Michigan, pers. comm.). Moreover, bloaters continued to remain abundant through the mid- to late-1980's. In 1985 and 1986, the bloater catch per unit effort was comparable to that observed in 1984; the 1987 CPUE exceeded that observed in 1984 (G. W. Eck, U. S. Fish and Wildlife Service, Ann Arbor, Michigan, pers. comm.). Young-of-the-year bloaters, which inhabit epilimnion and metalimnion, exert intense size-selective predation pressures on the zooplankton community, including *D. pulicaria* (Wells 1968; Crowder and Crawford 1984; Warren and Lehman 1988). Juvenile bloaters (age >2 yr) inhabit the metalimnion and also exert size-selective predation pressures on the zooplankton community. Thus, as bloater and alewife abundances increased over the mid- to late-1980's, predation pressures on the epilimnetic and metalimnetic zooplankton community probably increased, possibly leading to a decline in *D. pulicaria* abundances. Declines in *D. pulicaria* abundances also have been related to increased predation exerted by the predaceous cladoceran *Bythotrepes cederstroemi* which became established in Lake Michigan in 1986 (Lehman 1987). Others disagree with this hypothesis (Sprules et al. 1990).

Overall, the results of studies conducted in southeastern Lake Michigan in the 1970's and early 1980's and offshore of Grand Haven in later years indicate that improved water clarity as a consequence of top-down effects can be linked only to summer 1983 when *D. pulicaria* dominated zooplankton biomass (Scavia et al. 1986). However, later studies (Dorazio et al. 1987; Lehman 1988) have minimized the role *D. pulicaria* had in controlling summer phytoplankton abundances, including summer 1983. Similarly, although grazing experiments were not conducted, the results of the present study suggest that earlier changes in the abundance of large-bodied copepods (i.e. *L. macrurus* and *D. sicilis*) had no apparent influence on water clarity in southeastern Lake Michigan.

Other Factors: Lake Circulation

Two questions remain with regard to long-term trends in zooplankton abundances and water clarity in southeastern Lake Michigan. First, Why did *D. pulicaria* not become a species dominant in southeastern Lake Michigan during the late 1970's and early 1980's? Second, Why was there no apparent decrease in water clarity in the inshore region over summer 1982–84 when zooplankton biomass was 10% of earlier (1972–81) values (Evans 1986)? The answer to both questions may be based on the lake circulation patterns.

Lake Michigan is a physically dynamic system with complex circulation patterns. Flow patterns change over one time to another in response to changes in thermal regime and wind speed and direction (Ayers et al. 1958). Upwellings, large-scale gyre systems, and other flow patterns result in the strong mixing of waters from the northern and southern regions of the lake. Thus, not only are there inshore and offshore water exchanges, but whole-lake exchanges as well. Similarly, there is a strong exchange of zooplankton throughout the lake. Hence, in a given region (e.g. southeastern Lake Michigan), zooplankton community structure reflects the influence of lakewide events which have subsequently been modified by local events.

The lakewide decline in alewife populations was not strongly evident until 1983 (Fig. 1; Eck and Wells 1987). Consequently, *D. pulicaria* did not become strongly established in the offshore region until summer 1982 (Evans and Jude 1986); moreover, *D. pulicaria* did not become a major component of offshore summer zooplankton biomass until summer 1983 (Scavia et al. 1986). While conditions in the offshore region of southeastern Lake Michigan may have been hospitable for *D. pulicaria* as early as 1978 (as evident from the sporadic occurrence of this species in the zooplankton beginning in 1978), the constant dilution of this water with other regions of the lake (where alewife were abundant) probably prevented *D. pulicaria* from becoming a dominant species. Similarly, intense size-selective fish predation prevented *D. pulicaria* from becoming a species dominant in the inshore region during summers 1982–84 despite the strong inshore-offshore exchange of waters and zooplankton (Evans and Jude 1986).

The lakewide exchange of water appeared to exert less of a modifying influence on hypolimnetic zooplankton population trends in the offshore region of southeastern Lake Michigan; unlike *D. pulicaria*, long-term trends in *L. macrurus* and *D. sicilis* abundances appeared to be strongly affected by the regional decline in alewife. In order for *L. macrurus* and *D. sicilis* abundances to follow regional alewife population trends, alewives must have been more abundant in southeastern Lake Michigan than lakewide during the early 1970's; *L. macrurus* and *D. sicilis* transported into this region experienced an increase in predation pressures. As alewife abundances declined in southeastern Lake Michigan during the mid-1970's (while lakewide abundances remained unchanged), predation pressures on hypolimnetic copepods in this region declined. Hence, *L. macrurus* and *D. sicilis* transported into southeastern Lake Michigan experienced less intense predation

pressure than in earlier years. Predation pressures then increased in the late 1970's due to the regional and/or lakewide increase in bloater abundances; unlike alewife, the regional and lakewide increase in bloater abundance were separated by only one year.

The physical exchange of offshore waters may also have moderated water clarity in the inshore region of southeastern Lake Michigan during summer 1982–84. Intense yellow perch predation during this period, reduced inshore zooplankton biomass to 10% of earlier values (Evans 1986). However, despite this decrease in grazer biomass, phytoplankton biomass apparently did not increase substantially, though the evidence is circumstantial. First, there were no reports of increased nuisance algal blooms along public beaches or municipal water intakes. Second, zooplankton samples collected from the power plant intake in summer 1982–84 contained relatively small amounts of net phytoplankton (M. S. Evans, pers. obs.). The apparent failure for phytoplankton to "bloom" in the inshore in response to a 10-fold decline (1975–81 vs. 1982–84) in grazing pressure may be attributable to the strong exchange of "clear" offshore water with the more "turbid" inshore. This exchange may have been especially effective in summer 1983 and 1984 when water clarity in the offshore region was notably high (Scavia et al. 1986).

Top-Down Control as a Management Strategy for the Great Lakes

Recent changes which have occurred in the Lake Michigan ecosystem have provided support for the hypothesis that top-down management strategies may be a useful approach for improving water clarity and controlling algal abundances in this and other large lakes (Scavia et al. 1986; Kitchell et al. 1988). However, as researchers continued to investigate the changing Lake Michigan ecosystem (Dorazio et al. 1987; Lehman 1988; this study), new dimensions have been added to this hypothesis. Thus, several factors need to be explored in the further evaluation of the relative merits of top-down vs. bottom-up management strategies.

1) As a large lake, Lake Michigan supports a high diversity of planktivorous fish. Thus, as one species decreases in abundance, other species increase in abundance (Christie 1974; Jude and Tesar 1985; Eck and Wells 1987). Consequently, a decline in the abundance of one planktivorous fish species does not necessarily mean that predation pressures on the zooplankton community will decrease. In southeastern Lake Michigan, the zooplankton community exhibited a variety of responses to the long-term decline in alewife abundance. Increases in yellow perch, bloater, and rainbow smelt apparently compensated for decreases in alewife abundance. The net effect was that there were no major changes in zooplankton mean size and biomass. Consequently, there was no apparent top-down effect of declining alewife abundances on water clarity in the inshore or offshore region over 1972–82. Moreover, zooplankton biomass actually declined in the inshore region over summer 1982–84 as a direct consequence of increased yellow perch abundance; water clarity, however, apparently did not decrease.

2) Improvements in water clarity as an apparent result of top-down effects were limited to the offshore and to summer 1983. Intensified grazing was specifically attributed to large-bodied *D. pulicaria* which dominated zooplankton biomass during this summer (Scavia et al. 1986). However, water clarity was not improved in spring nor in autumn, seasons in which chlorophyll concentrations are highest (Ladewski and Stoermer 1973; Scavia et al. 1986). Moreover, although *D. pulicaria* persisted in the zooplankton community in later years, it apparently did not dominate the zooplankton biomass as in summer 1983. Consequently, it was no longer capable of controlling abundance increases of the summer epilimnetic phytoplankton community (Dorazio et al. 1987; Lehman 1988). Its apparent effects on the summer 1983 phytoplankton abundance also have been questioned (Lehman 1988).

3) The Lake Michigan ecosystem is dynamic, continuing to change in poorly understood and often unpredictable ways. For example, some fish species (e.g. the bloater) are capable of altering their resource utilization as a consequence of changing abundances of a major competitor (Crowder and Crawford 1984; Crowder and Magnuson 1982). Should these fish broaden their resource utilization with the decline in abundance of a major planktivorous competitor (e.g. the alewife), size-predation pressures on the zooplankton community would not necessarily decrease and could, in fact, increase. New predators may be introduced into the Great Lakes (e.g. *B. cederstroemi*), possibly counteracting the effects of declining abundances of a major fish planktivore. These unpredictable complexities in vertebrate and invertebrate predation make it extremely difficult to develop a successful long-term water quality management strategy based on top-down control.

4) Top-down management strategies for controlling phytoplankton abundance based on manipulating *Daphnia* populations may not be as effective in highly eutrophic as in mesotrophic systems. This is because *Daphnia* require an abundant and high-quality resource base in order to become a dominant species (Richman and Dodson 1983). Consequently, *Daphnia* may not become species dominants in eutrophic regions where unpalatable algae such as bluegreens dominate. Moreover, as total phosphorus concentrations increase, inedible algal abundance increases at a proportionately faster rate than edible algae (Watson and McCauley 1988). This suggests that zooplankton, including *Daphnia*, become increasingly less capable of controlling algal biomass with increasing lake productivity.

5) For large water bodies, lake circulation patterns can modify regional improvements (or degradations) in water clarity. In southeastern Lake Michigan, *D. pulicaria* remained rare over 1977–81 despite the major regional decline in alewife abundances; this region of the lake continued to be influenced by lake-wide events which prevented *D. pulicaria* from becoming strongly established until summer 1982. Similarly, the potential exists for semi-isolated embayments such as Green Bay to function as independent systems from the main body of the lake.

Summary

Improvements in maximum water clarity in the summer offshore waters of Lake Michigan appear to be linked to intensified grazing pressures exerted by the new dominant species, *D. pulicaria*: other large-bodied zooplankton which increased in abundance following the alewife population decline had no apparent effect on water clarity in southeastern Lake Michigan. The new dominance of *D. pulicaria* was dependent upon a number of conditions, not all of which can be assumed to continue in the future. Moreover, although *D. pulicaria* appeared to be capable of improving maximum water clarity in summer 1983, it apparently was not able to do so in later years and subsequent studies have questioned its grazing impact in sum-

mer 1983. Thus, it would not be prudent at this time to base phytoplankton control-strategies solely on top-down management strategies, although such strategies possibly may complement bottom-up control strategies. Moreover, top-down management strategies are probably more useful for moderately productive than for eutrophic systems and for small lakes rather than large and ecologically-complex systems such as the Great Lakes and the world's oceans.

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Reciprocal Diel Vertical Migration Behavior in Planktivores and Zooplankton in British Columbia Lakes

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Simultaneous comparison of planktivore and crustacean zooplankton distribution patterns in a set of British Columbia lakes suggested coupled diel vertical migration behavior in the two adjacent trophic levels. In lakes where juvenile sockeye salmon performed diel vertical migrations, most zooplankton were non-migratory and concentrated in shallow surface waters over the diel cycle. In contrast, in one lake where pelagic threespine sticklebacks were present, and where juvenile sockeye diel vertical migrations were periodically reversed, most zooplankton undertook diel vertical migrations. The presence of diel vertical migration behavior in zooplankton thus appears to be related to the presence or absence of the behavior in the predominant planktivores.

Une comparaison simultanée de la distribution temporelle d'organismes planctophages et de crustacés zooplanctoniques effectuée dans un ensemble de lacs de la Colombie-Britannique porte à croire qu'il y aurait migration verticale nycthémérale couplée chez ces deux groupes d'organismes appartenant à deux niveaux trophiques succesifs. Dans les lacs où il y a migration verticale nycthémérale des saumons rouges juvéniles, la plus grande partie du zooplancton ne migre pas et se concentre dans les eaux de surface peu profondes durant tout le nycthémère. Par contre, dans un lac où il y avait des épinoches à trois épines, et où la migration verticale nycthémérale des saumons rouges juvéniles était périodiquement interrompue, la plus grande partie du zooplancton commençait à effectuer une migration verticale nycthémérale. Ainsi, il semble que les migrations verticales nycthémérales du zooplancton soient reliées à l'existence ou à l'absence de telles migrations chez les organismes planctophages dominants.

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Diel vertical migration is a commonly observed behavior in both freshwater and marine zooplankton and there are many studies concerned with the documentation and biological interpretation of the phenomenon (reviewed by Cushing 1951; Hardy 1958; McLaren 1963; Hutchinson 1967; Longhurst 1976; Dingle 1980; and Bayly 1986). Several recent investigations suggest that such migrations in zooplankton serve as an adaptive compromise between the two antagonistic selective pressures of maximizing foraging intake for growth and/or egg production and minimizing spatial contact with visual-feeding planktivorous fish in surface waters (Kerfoot 1985; Giguere and Northcote 1987; Johnsen and Jakobsen 1987; Vuorinen 1987). By restricting surface ascents to nocturnal periods and spending daytime periods deep within the water column, zooplankton can achieve survival benefits (Zaret and Suffern 1976; Stich and Lampert 1981; Gliwicz 1986) which compensate for the reduced grazing opportunities at depth.

Diel vertical migrations are also common among planktivores in both freshwater (e.g. Narver 1970) and marine (e.g. Blaxter 1985) pelagic environments. Recent theory (Clark and Levy 1988) suggests that diel vertical migration in juvenile sockeye salmon (*Oncorhynchus nerka*) may also serve as a compromise whereby the migrants sacrifice feeding and growth opportunities in shallow water in return for decreased contact with visual-feeding piscivores (and therefore higher survival rates) in deep water. A vertically migrating planktivore will potentially negate a selective advantage of diel vertical migration by zooplankton. Clark and Levy (1988) considered three possible migratory strategies for zooplankton in the presence of a vertically migrating planktivore population: (1) refrain from diel vertical migration altogether and adopt a static, shallow distribution; (2) undertake reversed diel vertical migration; and (3) undertake nocturnal vertical migration so as to minimize visual contact with vertically migrating planktivores.

While diel vertical migration is the rule in numerous sockeye lakes (Levy 1987), there are exceptions to the usual behavior, such as within the glacially turbid Lake Tustumena on the Kenai Peninsula (Alaska) where diel vertical migrations of juvenile sockeye are reversed (Thorne 1983). Contrasting vertical migratory behaviors of juvenile sockeye within different nursery lakes provide an opportunity to test the predictions of Clark and Levy (1988) concerning zooplankton distribution and behavior in the presence of vertically migrating planktivores. In this paper, I describe zooplankton behavior in several British Columbia lakes where juvenile sockeye migrate vertically and also in one lake where planktivore (juvenile sockeye and threespine stickleback, *Gasterosteus aculeatus*) vertical migrations are periodically reversed. I then draw conclusions about the interrelationships of diel vertical migration behavior in zooplankton and planktivores.

Methods

Information on fish diel distribution and migration behavior was obtained using hydroacoustic methods (Thorne 1983b). Similar methods have been widely used for studying fish diel vertical migrations in pelagic environments (Hasler and Villemonte 1953; Northcote et al. 1964; Beamish 1966; Narver

FIG. 1. Location of study lakes within the province of British Columbia.

1970; Dembinski 1971; Begg 1976; Bohl 1980; Janssen and Brandt 1980; Hamrin 1986). Mathisen et al. (1977) have described juvenile sockeye as being ideally suited for acoustic enumeration because of their confinement to the limentic zone, their relatively simple size structure, the absence of a large number of co-habiting pelagic fish species, and the relatively simple physical properties of fresh water (compared to sea water).

Previous midwater trawling studies have shown that juvenile sockeye are numerically dominant in four of the lakes chosen for study (Fig. 1), including Babine (Narver 1970), Cultus (Burczynski and Johnson 1986), Shuswap (Enzenhofer and Hume 1989) and Quesnel (J. Hume, Department of Fisheries and Oceans, Cultus Lake Laboratory, Cultus Lake B.C. V0X 1H0, unpubl. data). Previous studies employing hydroacoustics in conjunction with trawl sampling (Narver 1970; Woodey 1972; Barraclough and Robinson 1972: McDonald 1973) justify a reliance on hydroacoustics alone within lakes where juvenile sockeye dominate numerically in order to document diel vertical migration behavior. Trawling has also shown both juvenile sockeye and threespine stickleback to be numerically dominant in the pelagic zone of Nimpkish Lake (K. Hyatt, Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, B.C. V9R 5K6, unpubl. data.).

A 420 kHz BioSonics echosounder equipped with a 15 degree transducer (−3db, full angle) was used to generate echo signals (0.4 ms pulse width at a rate of $2 \cdot s^{-1}$) which were digitized and taped on video cassette recorder (VCR) tape. The system was operated from a 5m, fiberglass boat with the transducer mounted on a rotatable pipe fixed to the side of the boat. When a relatively dense concentration of pelagic fish was located, it was tracked over a 24 h period. By transecting at a velocity of $2 m \cdot s^{-1}$ in an irregularly directed fashion, a large number of targets were encountered and electronic "surface noise" was minimized. Transects of 10 min duration were undertaken to characterize the vertical depth distribution of the fish at a given point during the diel cycle. At a later date, echograms were generated from the VCR tape with a BioSonics thermal chart recorder adjusted so that voltage threshold levels were 50 mV above ambient noise levels.

A hand-operated winch system, with a 5 kg weight, was employed to accurately position a temperature probe and a zooplankton pump intake. Using a YSI-SCT meter, single temperature profiles were measured at mid-day at 1-m depth intervals from the surface down to 50 m. Surface temperatures were also measured with a mercury thermometer, accurate to 0.1°C, to derive a correction factor (usually less than 0.5°C) which was applied to the vertical temperature profile. Two vertical zooplankton sampling series were taken on each sample date,

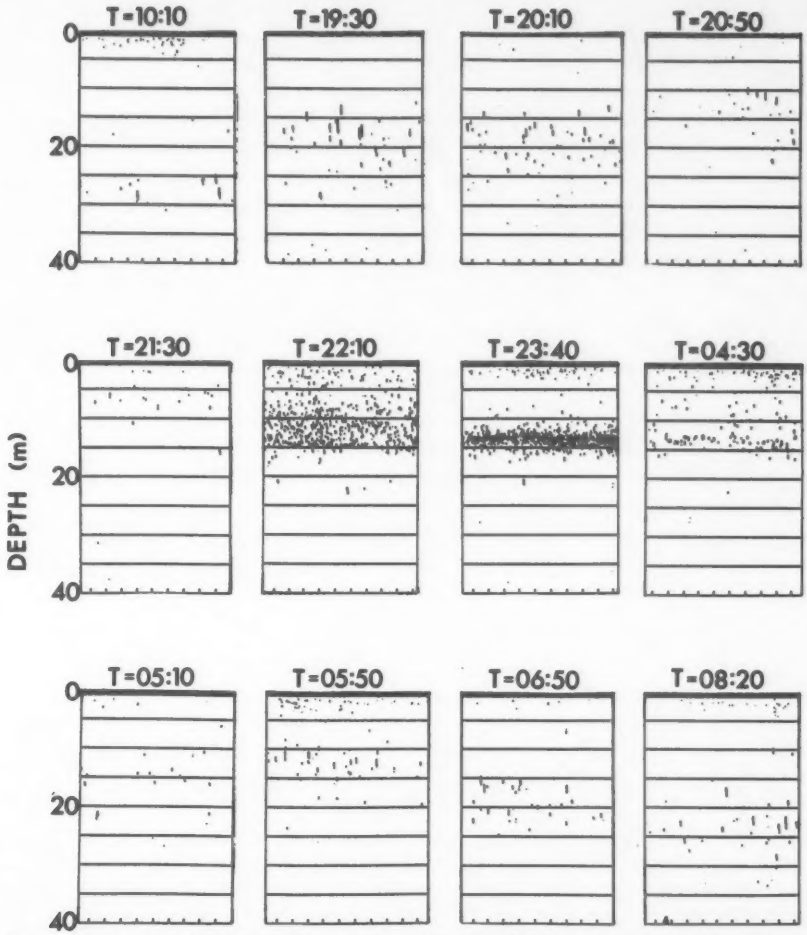


FIG. 2. Diel sequence of echograms showing migration of juvenile sockeye salmon within upper 40 m of Babine Lake on Aug. 19–20, 1986. Numbers above echograms indicate time of sampling (PDST).

the first at mid-day, and the second during the middle of the night.

Replicate 75 L zooplankton samples were taken at five depths (1, 7, 15, 22, and 30 m) using a Par diaphragm pump which sampled by suction from the surface. The pump was equipped with a funnel on the intake which was attached to the winch cable and lowered to the desired sampling depth. Because of observed variation in pump delivery rate, water was pumped initially into a 75 L vessel and then siphoned through a 100 μm plankton net. After concentrating the organisms in a small volume of water, the animals were poured into a glass jar and preserved in approximately 5% sugared formalin.

In the laboratory, the preserved specimens were concentrated on a 100 μm mesh Nitex sieve and transferred to a gridded counting vessel for enumeration under a stereo microscope at 10× magnification. All crustacea were identified to genus, and enumerated to compute the density of organisms·m^{-3}. Copepod nauplii were subsampled during the counting procedure by counting a subset of 14 (out of 84) regularly spaced grid squares.

Results

During mid-summer 1986, juvenile sockeye in Babine Lake undertook diel vertical migrations (Fig. 2) similar to those reported by Narver (1970) and McDonald (1973). During daylight periods, schooled fish targets were present on echograms at depths between 25 and 35 m. At dusk, the schools ascended close to the surface, as evidenced by a decrease in echo target frequency due to near-field effects ($T = 2050$ and $T = 2130$ on Fig. 2). The presence of juvenile sockeye in shallow surface waters of Babine Lake during early evening twilight periods has been verified by Johnson (1956) who obtained maximum sockeye catches in surface tow nets during this portion of the diel cycle. At night, the schools dispersed ($T = 2210$) and the fish gradually occupied a discrete vertical position in the water column between 10 and 15 m ($T = 2340$). At dawn the pattern reversed when the fish first ascended ($T = 0430$ and $T = 0510$) and then later descended ($T = 0650$ and $T = 0820$) to their daytime depth. Diel echogram series, showing a general pattern similar to those shown in Fig. 2, were also obtained on June 25–26, Aug. 1–2, and Oct. 14–15, 1986.

There were seasonal changes in juvenile sockeye nocturnal vertical distribution. In Shuswap Lake (Fig. 3), juvenile sockeye occupied deeper depths and also a wider nocturnal depth range as the summer and fall progressed. These changes coincided with the seasonal formation and progression of the ther-

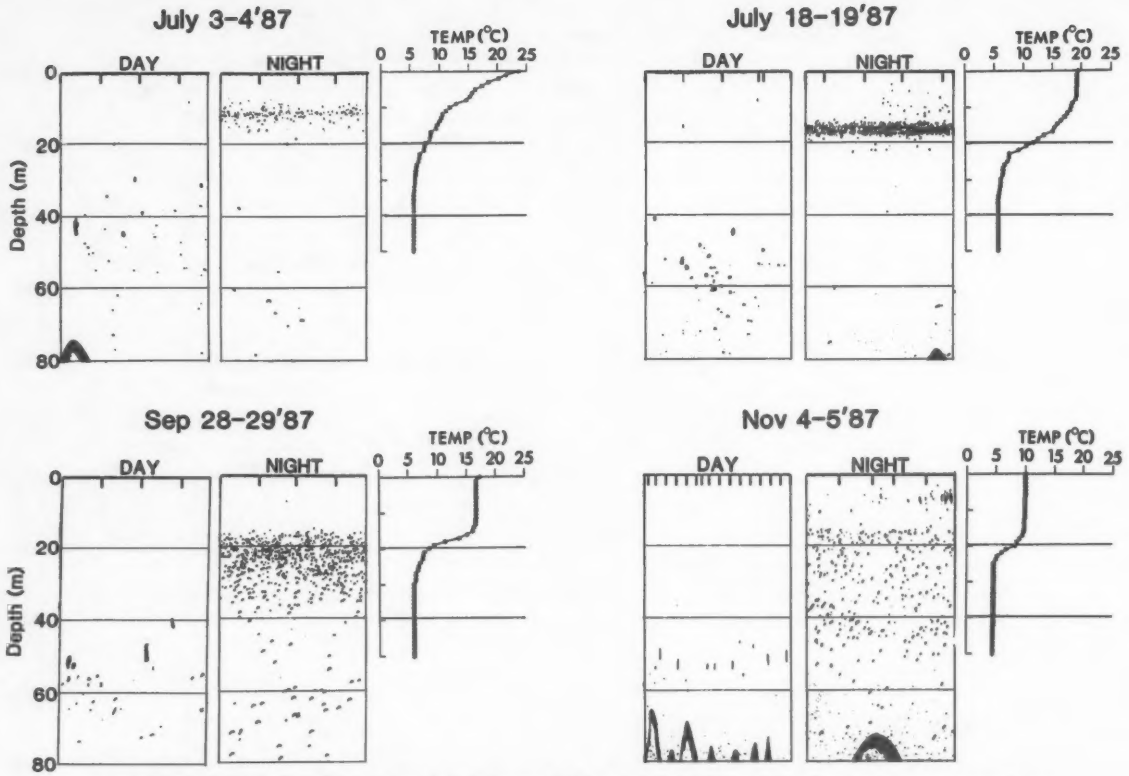


FIG. 3. Day and night echograms obtained from Shuswap Lake during 1987, shown in relation to the temperature profiles.

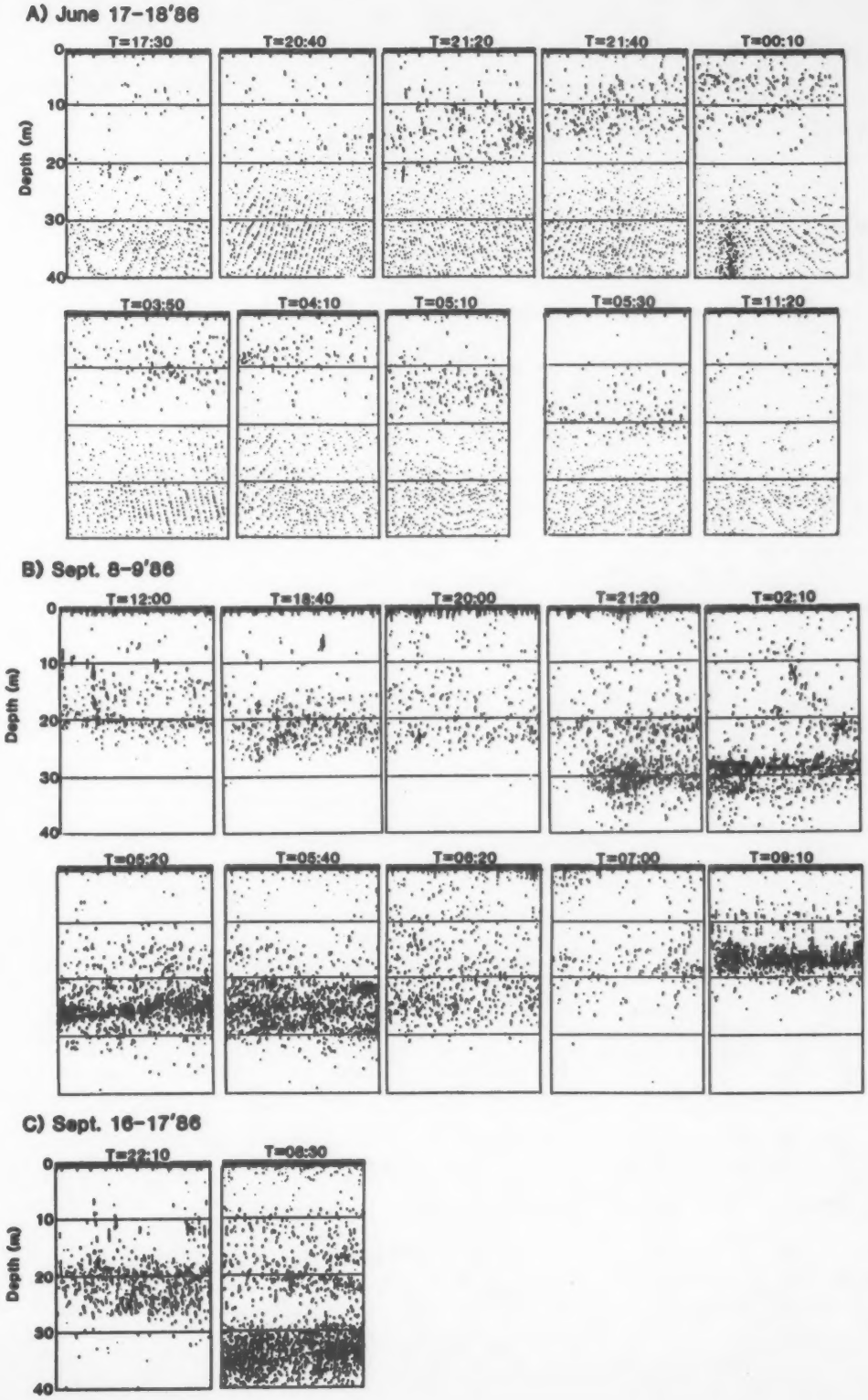
mocline in the water column of Shuswap Lake (Fig. 3). Evidence for an effect of temperature on juvenile sockeye nocturnal depth position is provided by Levy (1990).

Juvenile sockeye also undertook diel vertical migrations in Cultus (Johnson and Burczynski 1985) and Quesnel (Clark and Levy 1988) lakes. At Nimpkish Lake, diel movements of pelagic fish targets (both sticklebacks and juvenile sockeye were present) were reversed for at least a portion of the year (Fig. 4). On the first survey date in June 1986, there was a group of echo targets which migrated vertically in a normal diel fashion. However, on two separate dates during September 1986, diel vertical migrations were reversed such that most targets were deeper during the night than during the day (Fig. 4). Although the combined occurrence of sticklebacks and juvenile sockeye in Nimpkish complicates the interpretation of echograms from this lake (Fig. 4), it is unlikely that juvenile sockeye were undertaking vertical migrations with the usual diel timing (deep during the day, shallow at night) during September of 1986. Rather, a reversed juvenile sockeye diel vertical migration would be consistent with the observed September echogram sequences.

Zooplankton pump sampler results from Babine Lake (Fig. 5) suggested a static diel vertical depth distribution of all crustacean genera except *Bosmina*, which undertook reversed diel vertical migrations on the two dates studied. Zooplankton from Babine Lake have also been sampled by Narver (1970) using Miller net samplers, which by virtue of their rapid, towed deployment (Andersen and Narver 1968) accurately sample large crustacean zooplankton. Pump sampling produced results similar to those obtained by Narver (1970) with one notable exception: *Heterocope septentrionalis* were absent from daytime pump samples, and were only captured incidentally at night. *Heterocope* is a large (2–3 mm) predatory copepod, evidently capable of avoiding capture by the pump sampler. Narver's (1970) results showed a diel vertical migration of *Heterocope*, a static vertical distribution of other copepods and *Daphnia*, and a reversed diel vertical migration of *Bosmina*.

Zooplankton pump sampler results also indicated static (nonmigratory) zooplankton populations in Cultus, Quesnel, and Shuswap Lakes (Fig. 6). The occasional minor diel difference in depth distribution pattern can be ascribed to sampling error, rather than active vertical migration. Juvenile sockeye within these three lakes undertook diel vertical migrations, and occurred in dense numbers in two of the systems (Quesnel in 1986, Shuswap in 1987). Zooplankton in Shuswap Lake in June and September of 1987 (corresponding to respective time periods before and after juvenile sockeye had recruited into the pelagic zone of the lake) indicated no evidence of diel vertical migration during either of these time periods (Fig. 6).

The presence of planktivores in shallow waters by day should exert a strong selective pressure for zooplankton to avoid the euphotic zone during daylight periods and perform diel vertical migrations. This prediction was tested by comparing the diel vertical movements of zooplankton within Nimpkish Lake (Fig. 7) where fish (both sticklebacks and juvenile sockeye were present) vertical migration patterns were periodically reversed (Fig. 4). Most of the dominant zooplankton within Nimpkish Lake, including *Bosmina*, *Diaptomus*, and *Daphnia*,


A) June 17–18'86
T=17:30
T=20:40
T=21:20
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T=00:10
T=03:50
T=04:10
T=05:10
T=05:30
T=11:20
B) Sept. 8–9'86
T=12:00
T=18:40
T=20:00
T=21:20
T=02:10
T=05:20
T=05:40
T=06:20
T=07:00
T=09:10
C) Sept. 16–17'86
T=22:10
T=06:30
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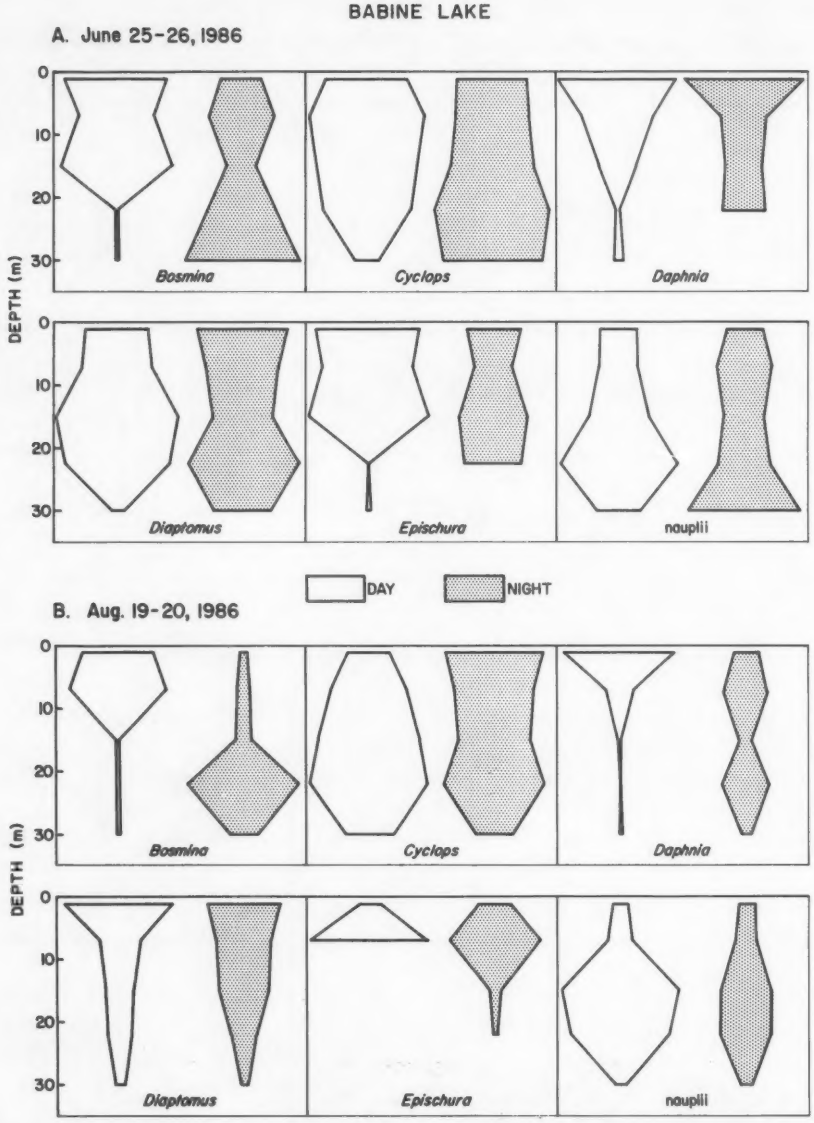

FIG. 5. Day and night vertical depth profiles of the predominant crustacean zooplankton species captured in plankton pump samples from Babine Lake on 2 dates during 1986. Kites depict the relative abundance of organisms at 5 particular depths throughout the upper 30 m of the water column.

undertook diel vertical migrations. Two genera (*Epischura* and *Cyclops*) were also distributed in shallower water at night than during the day (Fig. 7); however, diel movements of the latter two genera were not as pronounced as those of the former.

Discussion

Results from the present study indicate that diel vertical migration behavior in crustacean zooplankton may be linked with the presence or absence of the behavior in planktivores. Zooplankton was largely static in lakes where sockeye juveniles undertook diel vertical migrations. Within Nimpkish Lake, where vertical migrations by juvenile sockeye (and/or sticklebacks) were periodically reversed, zooplankton undertook diel vertical migrations.

There are at least two possible explanations for a reversal of diel vertical migration behavior by juvenile sockeye in Nimpkish Lake. First, there could be a low predator-induced mor-

FIG. 4. Diel echogram sequences from Nimpkish Lake on (A) June 17–18, (B) Sept. 8–9, and (C) Sept. 16–17, 1986. Echogram marks between 20–40 m on June 17–18 caused by electrical noise. Numbers above echograms indicate time of sampling (PDST).

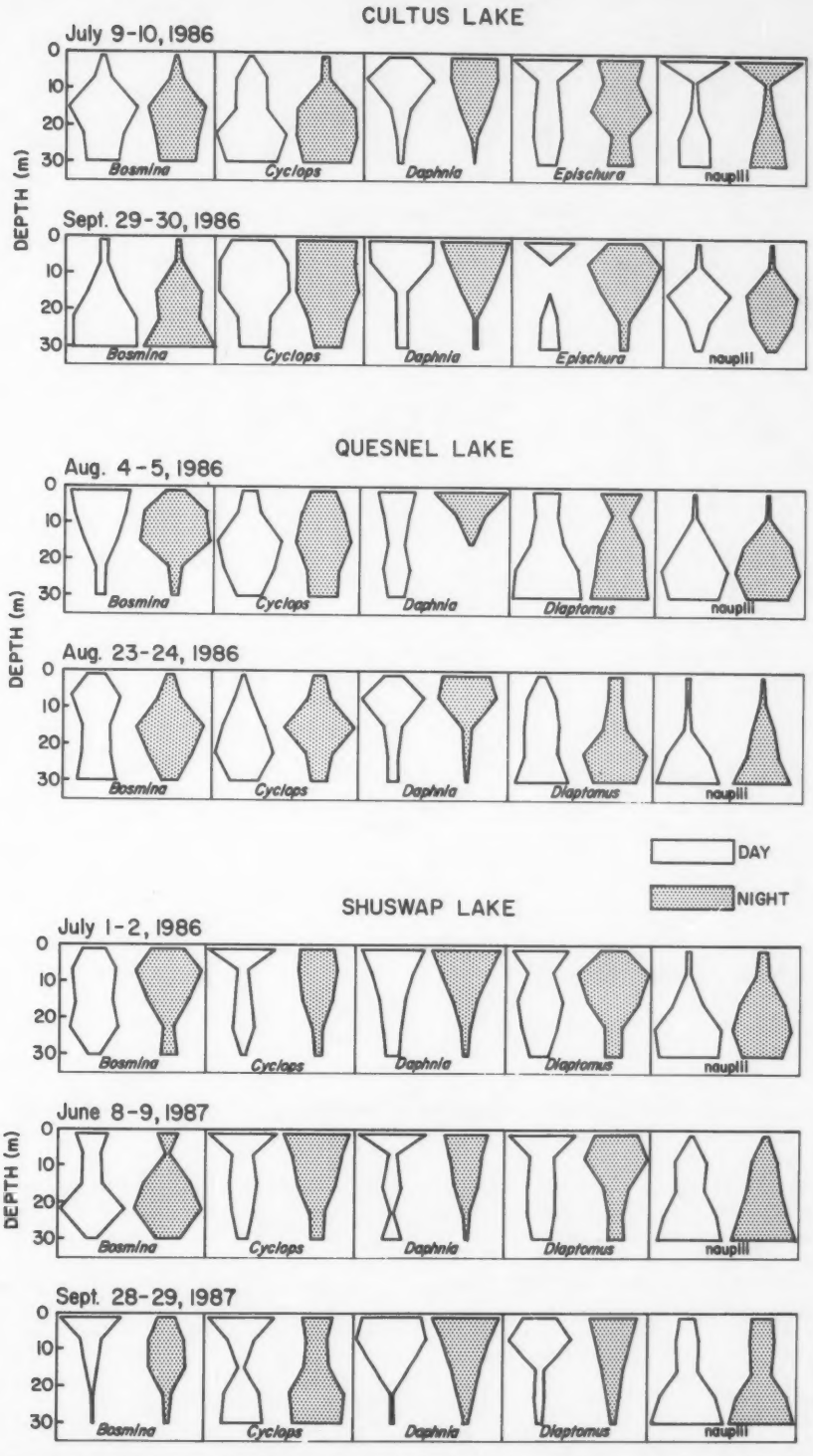

FIG. 6. Day and night vertical depth profiles of the predominant crustacean zooplankton species captured in plankton pump samples from Cultus, Quesnel, and Shuswap lakes.

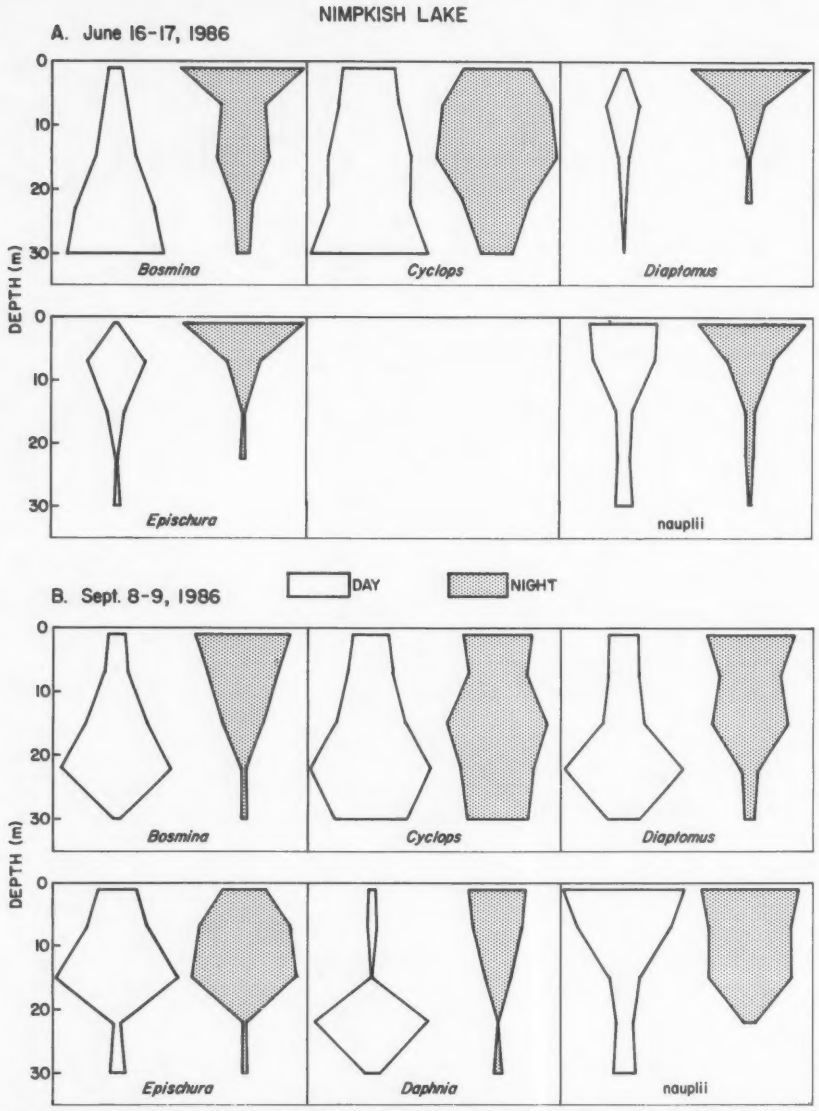

FIG. 7. Day and night vertical depth profiles of the predominant zooplankton species captured in plankton pump samples from Nimpkish Lake on 2 dates during 1986.

tality rate since few predators have been observed within the pelagic zone, relative to other sockeye nursery lakes (K. Hyatt, Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, B.C. V9R 5K6, unpubl. data). Second, the presence of threespine sticklebacks might cause juvenile sockeye to reverse their migrations within Nimpkish Lake. Pelagic sticklebacks are planktivorous and have been shown to compete with juvenile sockeye in enclosure experiments conducted at Kennedy Lake (O'Neill and Hyatt 1987). It is presently difficult to reject either explanation.

In the presence of non-migratory planktivores, freshwater zooplankton often undertake diel vertical migrations (Zaret and Suffern 1976; Stich and Lampert 1981; Gliwicz 1986). However, in the presence of a vertically migrating planktivore like juvenile sockeye salmon, there is no selective advantage for zooplankton to migrate vertically, and the animals maintain a static distribution in shallow water. *Daphnia longispina*, for example, is a cladoceran which migrates vertically within Lake Kvernavatn, Norway, in order to balance predator avoidance and the risk of starvation (Johnsen and Jakobsen 1987). *Daphnia*, including *D. longispina* (Johnson 1965), maintain a shallow, static distribution within Babine Lake where their main predators, juvenile sockeye salmon, perform diel vertical migrations.

The cladoceran *Bosmina coregoni* serves as prey for juvenile sockeye (Doble and Eggers 1978; Levy and Hall 1985; Kyle et al. 1988) as well as the predatory, contact-feeding copepod, *Heterocope septentrionalis* (O'Brien and Schmidt 1979). The

absence of *Bosmina* from arctic ponds has been attributed to predation from *Heterocope* (Luecke and O'Brien 1983). Within British Columbia sockeye lakes, three different migratory patterns were displayed by *Bosmina:* static, vertical migration, or reversed vertical migration. *Bosmina* populations were static in Cultus, Quesnel, and Shuswap Lakes where sockeye migrated vertically. Within Nimpkish Lake, where sockeye vertical migrations were reversed and where sticklebacks were present, *Bosmina* undertook vertical migrations. Within Babine Lake, *Bosmina* was a reversed vertical migrator, presumably in order to minimize its spatial overlap with *Heterocope,* which undertakes a diel vertical migration covering 15–25 m (Narver 1970).

The low number of *Heterocope* in zooplankton samples during the present study was probably a sampling artifact due to pump intake avoidance. It is unlikely that *Heterocope* densities have been reduced due to the increased juvenile sockeye grazing pressure associated with the construction of three sockeye spawning channels in the late 1960's (Levy and Hall 1985). Rankin (1977) did not detect reduced *Heterocope* abundance in zooplankton samples obtained prior to (1958–62) and after (1973–74) construction of three major spawning channel facilities on tributaries of Babine Lake.

The documented vertical migrations of *Heterocope* within Babine Lake (Narver 1970) are likely a response to predation by juvenile sockeye. *Heterocope* in Babine presumably enter shallow surface waters at night in order to minimize contact with the vertically migrating sockeye juveniles. The reversed vertical migrations of *Bosmina* in Babine would effectively segregate them from the vertically migrating *Heterocope*. *Bosmina* are also susceptible to predation by sockeye juveniles; however, due to their respective densities, *Heterocope* would exert a more severe predation mortality than sockeye, and provide a strong selective pressure for *Bosmina* to avoid surface waters at night. Similar conclusions concerning the reversed vertical migration behavior of *Bosmina* were reached by Zaret (1980, page 77).

Results of the present study suggest that freshwater zooplankton may adopt a static vertical distribution in the presence of vertically migrating planktivores. Pijanowska and Dawidowicz (1987) attributed the lack of vertical migration of *Daphnia* in two Polish lakes to a homogeneous seston distribution. However, two out of three planktivores present within the lakes (*Coregonus albula* and *Osmerus eperlanus*) can be vertical migrators (Northcote and Rundberg 1970; Dembinski 1971). An alternative interpretation is that *Daphnia* within these two lakes are non-migratory because planktivorous predators undertake diel vertical migrations. Under these circumstances, there would be no selective advantage for *Daphnia* to migrate vertically.

Cascading trophic interactions (Carpenter et al. 1985; McQueen et al. 1986) provide a useful perspective for the interpretation of aquatic community relationships within the pelagic environments of lakes and oceans. In addition to grazing-related effects, there can also be cascading behavioral interactions between trophic levels. The present study suggests that the presence of diel vertical migration behavior in zooplankton depends upon the presence or absence of the behavior in juvenile sockeye salmon. In turn, diel vertical migration in juvenile sockeye may serve as a piscivore avoidance mechanism (Eggers 1978), effectively optimizing the trade-off between zooplankton foraging and predator avoidance (Clark and Levy 1988). These behavioral interactions which extend across three (or more) trophic levels undoubtedly have important consequences for the pelagic community.

Acknowledgements

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Density-Dependence at Sea for Coho Salmon (*Oncorhynchus kisutch*)

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Emlen, J. M., R. R. Reisenbichler, A. M. McGie, and T. E. Nickelson. 1990. Density-dependence at sea for coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. 47: 1765–1772.

The success of expanded salmon hatchery programs will depend strongly on the degree of density-induced diminishing returns per smolt released. Several authors have addressed the question of density-dependent mortality at sea in coho salmon (*Oncorhynchus kisutch*), but have come to conflicting conclusions. We believe there are compelling reasons to reinvestigate the data, and have done so for public hatchery fish, using a variety of approaches. The results provide evidence that survival of these public hatchery fish is negatively affected, directly by the number of public hatchery smolts and indirectly by the number of private hatchery smolts. These results are weak, statistically, and should be considered primarily as a caution to those who, on the basis of other published work, believe that density-dependence does not exist. The results reported here also re-emphasize the often overlooked point that inferences drawn from data are strongly biased by investigators' views of how the systems of interest work and by the statistical assumptions they make preparatory to the analysis of those data.

La réussite des programmes élargis de piscifacture pour les saumons dépendra fortement du taux de retours à la baisse induit par la densité par smolt libéré. Plusieurs auteurs ont abordé la question de la mortalité en mer en fonction de la densité du saumon coho (*Oncorhynchus kisutch*), mais ils en sont arrivés à des conclusions contradictoires. Nous croyons qu'il y a des raisons contraignantes pour réexaminer les données, et nous l'avons fait pour des poissons de piscifacture publique au moyen de différentes approches. Les résultats ont montré que la survie des poissons de piscifacture publique compromise directement par le nombre de smolts de piscifacture publique et indirectement par le nombre de smolts de piscifacture privée. Ces résultats sont statistiquement faibles, et devraient être considérés surtout comme un avertissement pour ceux qui, d'après d'autres travaux publiés, croient que la dépendance en fonction de la densité n'existe pas. Les résultats présentés ici mettent aussi de nouveau l'accent sur le point souvent peu considéré que les conclusions tirées des données sont fortement biaisées par les opinions des chercheurs sur la façon dont les systèmes d'intérêt fonctionnent et par les hypothèses statistiques qu'ils ont formulées en vue de l'analyse de ces données.

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The extensive and expensive efforts directed at freshwater habitat and passage improvement for anadromous salmonids, as well as current hatchery production, are based on the tacit assumption that populations of salmon are limited primarily by availability of the freshwater habitat for spawning and rearing (fish passage is considered density-independent). Yet, although the gravel dumping, log felling, and other activities designed to improve habitat appear to have met with some success, the results have not been adequately quantified, nor the impact of the various constituent activities individually identified. Since the 1960's, both hatchery operations and runs of hatchery fish have increased for coho salmon (*Oncorhynchus kisutch*) in the Oregon–Washington coastal area. But there is no clear evidence that the two trends are causally related. Clearly, one need for salmon management is to address rigorously the assumption that population limitation acts only in freshwater habitat. Is there, in fact, density-related mortality at sea? If so, what is its importance for determining return rates?

Density-dependent mortality of coho salmon at sea has been addressed by several investigators (Peterman 1982; Clark and McCarl 1983; McCarl and Rettig 1983; McGie 1984; Nickelson 1986). Using estimated numbers of smolts and returning adults (escapement plus catch) for the period 1960–81 for the Oregon Production Index Area (OPIA)[2], McGie (1984) concluded that density-dependent mortality was important in years of low upwelling, but absent in years of high upwelling. McCarl and Rettig (1983) also found evidence for density-dependence in OPIA coho salmon for the years 1958–79, using the method of Just and Pope (1978, 1979) to adjust for unknown error structure. Nickelson (1986), however, challenged these claims. Pointing out that wild fish have higher survival than hatchery fish, and that the proportions of hatchery to wild fish have increased greatly over the years, he noted that both McGie's (1984) and McCarl and Rettig's (1983) results, based on pooled data for wild and hatchery fish, could be misleading. Reanalysis of the data, considering wild, public hatchery and private hatchery fish separately (i.e. as though they do not occur together at sea), provided no evidence for density-dependent

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[2]The Oregon Production Index Area (OPIA) is a portion of the Pacific coastal water bounded on the north by Leadbetter Point, WA, and to the south by Monterey Bay, CA. (see Nickelson 1986).

mortality at sea (Nickelson 1986). See also Clark and McCarl (1983).

Despite the plethora of analyses, we feel strongly that a re-examination of the data is warranted. This assertion is based on the following:

1) Our experience with managers and fishery biologists, generally, leads us to believe there is a consensus of no density feedback, based on Nickelson's work as the last word. It is our view that the last word has not been written, but that this is not adequately recognized and needs further emphasis.

2) All of the above-cited papers are based on assumptions either that fish from different sources (private or public hatchery, or wild/natural) mix in the near-sea area, or that they don't. Inasmuch as the different assumptions appear to support opposite inference, there is a need to examine these assumptions.

3) All of the above analyses used simple, empirical expressions; none was based on a model derived explicitly for the situation at hand, using biological criteria. Occasionally, though not always, use of different models leads to different inferences about the importance of some relation. We derive two, alternative models based on different, biological assumptions to test this possibility.

4) Inasmuch as size-related mortality, growth rate, and possibly other, biological processes affecting survival at sea are undoubtedly functions of sea conditions (upwelling and temperature), we feel these variables should be included, explicity, in the models used to test for density-dependence. This has not been done previously.

5) Several of the above-cited papers noted that inferences drawn (vis-à-vis rejecting or failing to reject the null hypothesis of no density-dependence) might depend on assumptions about the form of the statistical error. None of them, however, looked carefully at the structure or causes of the error. Indeed, it was not possible for them to do so except in the context of the purely empirical model employed.

6) Several corrections have been made in the data set used by the previous authors (A. McGie, Oregon Dept. Fish and Wildlife, Corvallis, OR, pers. comm.), and there are now 5 yr of additional data (Table 1).

To address point 2, above, concerning whether analysis should lump stocks of different origin, we first note that the concensus is that density-dependence at sea, if it occurs, takes place very early, probably within the first few weeks (see, e.g. Gunsolus 1978; Peterman 1982, 1987; Fisher and Pearcy 1988). The pertinent question, then, is whether wild, public and private hatchery fish mix during this period. If they do, then McGie's (1984) analysis, so far as it goes, is appropriate. If, in addition, his implied assumption is correct, that interactions among stocks are of the same form and magnitude as interactions within stocks we may conclude that density-dependence does occur at sea. If not, then further analysis is warranted.

We examined Pearcy's Cruise Reports for 1981 through 1985 (Ref. 81–13, 83–2, 84–2, 85–2, 85–14, Studies of Juvenile Salmonids off the Oregon and Washington Coast, Oregon State University Sea Grant College Program). A review of all individual tows in which at least two marked juveniles had been recovered indicated that a null hypothesis of 10% mixing or more (10% or more of one stock ends up in association with another) can be rejected at the $P = 0.185, 0.190, 0.194, 0.107$ levels for 1981, 1983, 1984, and 1985, respectively. The chance of so little mixing over all 4 yr is 0.0007. Inasmuch as Pearcy's samples swept several hundred thousand cubic feet, surely a volume much greater than that within which individual fish interact, the conclusion of little or no mixing is futher strengthened. Thus, analysis should proceed as if no mixing occurs. This is convenient for the reason that inaccuracies for wild fish, and the short time sequence of data for private hatchery fish make only the public hatchery data reliable. Accordingly, our analysis dealt with public hatchery data.

Form of the Model

In their respective analyses, both Peterman (1982) and Nickelson (1986) used the following model:

$$(1)\quad A(t) = \gamma S(t-1)^k e^{\epsilon}$$

where $A(t)$ is adult returns in calendar year t, and $S(t-1)$ is the corresponding smolt population in calendar year $t-1$. The coefficient γ describes the proportion of smolts surviving density-dependent and density-independent influences, k reflects density-dependence, and ϵ is a random error term (after Peterman 1981). McCarl and Rettig (1983) used the same expression, while dealing with the error term in a more sophisticated fashion. While equation (1) is, perhaps, convenient, it has no clear biological basis — it is not possible to list the assumptions or simplifications which underly it. It is purely empirical.

McGie's (1984) model was a Ricker (1954) relation,

$$(2)\quad A(t) = S(t-1)\exp\{-S(t-1)\}e^{\epsilon}$$

which is biologically based, but not necessarily appropriate for our present use.

There seems little doubt that coho salmon dynamics can be described crudely with equation (2). However, the descending limb of the Ricker curve, as usually derived, follows from a density relation involving effects of adult fish, direct or indirect, on the number of eggs laid, survival of the eggs, or survival of the fry. Once the smolt stage is reached, it seems more likely that subsequent mortality through any time interval will depend on the population density experienced by the fish during that interval. If this is so, the smolt-to-return survivorship vs. initial (smolt) density is of the Beverton–Holt form. If, indeed mortality varies continuously with population density, we have Model 1.

Model 1

$$(3)\quad \text{Instantaneous Mortality } (=M) = -\frac{1}{n}\frac{dn}{dt} = \delta_o + \delta n$$

where n is the number of fish, δ_o is density-independent, and δn is density-dependent (proportional to population density) instantaneous mortality rate. Both δ and δ_o may be functions of age (t), of the form $\left\{\begin{matrix}\delta = \delta f(t) \\ \delta_o = \delta_o f(t)\end{matrix}\right\}$ where $f(t)$ is arbitrary except for the provison that it be continuously differentiable in t. Define $u = 1/n$, $d\theta = f(t)dt$. Then equation (3) becomes

$$du/d\theta = \delta_o u + \delta,$$

from which

$$u(t) = \left[u(0) + \frac{\delta}{\delta_o}\right] e^{\delta_o \theta(t)} - \frac{\delta}{\delta_o}.$$

Substituting for n, we obtain,

TABLE 1. Record of coho salmon smolt abundance, subsequent survival, and environmental conditions in year of sea entry (Oregon Department of Fish and Wildlife, unpublished data). U, T, and UT denote upwelling, sea surface temperature,and the cross product, respectively.

	Smolts released (millions)			Fraction surviving			Physical variables		
Year class	Wild	Public hatchery	Private hatchery	Wild	Public hatchery	Private hatchery	*U*	*T*	*UT*
1961	5.7	7.4	0	0.163	0.029	0	3.71	1.16	4.303
1962	8.5	16.6	0	0.092	0.022	0	2.65	1.20	3.18
1963	6.9	17.4	0	0.070	0.053	0	4.30	1.14	4.902
1964	8.3	25.6	0	0.137	0.039	0	3.61	1.19	4.295
1965	8.4	20.8	0	0.111	0.072	0	6.36	1.11	7.059
1966	7.7	23.8	0	0.114	0.071	0	7.65	1.11	8.491
1967	7.7	27.4	0	0.086	0.090	0	7.64	1.14	8.709
1968	8.5	27.8	0	0.074	0.064	0	8.19	1.17	9.582
1969	8.3	24.3	0	0.050	0.057	0	6.44	1.16	7.470
1970	8.8	32.4	0	0.072	0.075	0	6.52	1.17	7.628
1971	8.1	29.6	0	0.177	0.086	0	7.09	1.08	7.657
1972	6.6	36.0	0	0.098	0.042	0	4.24	1.09	4.621
1973	8.2	36.6	0	0.087	0.039	0	5.40	1.16	6.264
1974	8.2	34.5	0	0.083	0.074	0	7.91	1.16	9.175
1975	6.1	33.5	0.1	0.107	0.038	0	6.04	1.16	7.006
1976	6.8	35.3	0.1	0.184	0.085	0	7.44	1.08	8.035
1977	6.5	33.9	2.1	0.070	0.021	0	5.24	1.11	5.816
1978	7.1	37.5	2.4	0.054	0.041	0.006	6.13	1.20	7.356
1979	7.1	39.3	9.9	0.091	0.027	0.011	4.81	1.25	6.012
1980	3.9	34.6	5.8	0.090	0.029	0.016	3.85	1.23	4.735
1981	4.4	34.0	14.8	0.073	0.027	0.017	5.93	1.16	6.878
1982	7.5	37.8	23.9	0.042	0.029	0.012	4.81	1.19	5.723
1983	5.9	32.5	23.1	0.042	0.014	0.010	4.41	1.14	5.027
1984	4.6	30.9	16.3	0.060	0.019	0.009	1.77	1.24	2.194
1985	6.5	35.2	10.9	0.046	0.017	0.035	4.06	1.18	4.790
1986	3.7	32.5	8.6	0.074	0.069	0.063	3.11	1.17	3.638

Survival over critical period

$$= \frac{e^{-\delta_o \theta}}{1 + \frac{\delta\hat{\theta}}{\delta_o \hat{\theta}}(1 - e^{-\delta_o \theta})n_o} : \hat{\theta} = \theta(\hat{t}).$$

This is of the form, survival $= \dfrac{e^{-A}}{1 + \frac{B}{A}(1 - e^{-A})n_o}$

To convert this survival measure to that derived from adult return data, one must multiply it times the proportion of fish (still alive after the critical period) that do not return as jacks, and by the fraction of these fish that survive the subsequent year. Because the ratio of jacks in year y to the number of adults in year $y + 1$ varies little over years (Comprehensive Plan for Production and Management of Oregon's Anadromous Salmon and Trout, Part II. Coho Salmon Plan, Oregon Department of Fish and Wildlife, Fish Division, Anadromous Fish Section, June 1982), we write the product of these corrective factors as p^*, where $0 \leq p^* \leq 1$ is presumed independent of density and ocean conditions prevailing during the earlier, critical period. Survival from release to return (p) is then,

$$(4) \quad p = p^* \frac{e^{-A}}{1 + \frac{B}{A}(1 - e^{-A})n_o}$$

Harvest fraction estimates showed little annual variation in p^* between 1969–82 (mean = 0.724, SD = 0.073 for "late" stock coho salmon; mean = 0.494, SD = 0.100 for "early" coho salmon — Stock Assessment of Columbia River Anadromous Salmonids, Volume II, Coho, Sockeye, Chum Salmon, 1984, Oregon Department of Fish and Wildlife, Washington Department of Fisheries, Washington Department of Game, Idaho Department of Fish and Game, U.S. Department of Energy Bonneville Power Administration). Accordingly, we treated p^* as a constant to be statistically estimated.

Model 2

Our second model is based on a quite different assumption. Rather than supposing density to affect mortality, suppose it adversely impacts growth rate, prolonging the period of high, density-independent mortality. In this model there is no density-dependent mortality, per se. We write, for the early, critical period (of duration t),

$$(5) \quad -\frac{1}{n}\frac{dn}{dt} = \delta_o$$

where δ_o varies with ocean conditions as in Model 1. The proportion of fish returning as adults times the subsequent fraction surviving is again denoted by p^*. Equation (5) yields

$$(6) \quad \text{Survival} = p = p^* e^{-\delta_o t}.$$

In this model, the value of t is presumed to be related to body growth rate. For example, if predation is a source of mortality and occurs during a "window of vulnerability" that closes when the fish reach some critical size (Parker 1971), the age at which that size is reached (t) depends on growth rate.

To find t, we write the Von Bertelanffy growth equation,

(7) $dL/dt = a - bL : L =$ linear dimension,

Inasmuch as the critical period during which density-dependence may occur is presumably early, encompassing ages when growth is still well described by the ascending limb of the growth equation, the influence of the b term is small, and we can write

(8) $dL/dt = a$

But a, the growth rate, will vary with population density. For example, write

(9) $a = \bar{a}(1 - \xi n)$

Then,

$$dL/dt = \bar{a}(1 - \xi n) = \bar{a}(1 - \xi n_o e^{-\delta_o t})$$

The general solution to the above is

(10) $$L_i - L_o = \bar{a}\hat{t} + \frac{\bar{a}\xi}{\delta_o}(n_i - n_o)$$

Now, survivorship from release to return averages about 5% (Table 1). Therefore, n_t is considerably smaller than n_o, and equation (10) can be approximated with

$$L_i - L_o \simeq \bar{a}\hat{t} - \frac{\bar{a}\xi}{\delta_o} n_o$$

so that

$$\hat{t} \simeq \left[(L_i - L_o) + \frac{\bar{a}\xi}{\delta_o} n_o\right] / \bar{a}$$

which is of the form

(11) $\hat{t} \simeq \mu + \mu' n_o$

The value of L_t will probably change with t, since the predators are presumably also growing (Parker 1971). However, for a given set of predators, physical conditions, growth rate ($\bar{a}$), and density factor (μ), there will exist some L at which the window of vulnerability closes. The age at which that occurs is given by equation (11).

Finally, then (equation (6)),

(12) $$p = p^* \exp\{-\mu\delta_o(1 + \frac{\mu'}{\mu} n_o)\} \equiv p^* \exp\{-C(1 + Dn_o)\}$$

This is a Ricker relation, with $\alpha = p^* e^{-\mu\delta_o} = p^* e^{-C}$, and $\beta = \delta_o\mu' = CD$.

Incorporation of Environmental Variables

As reviewed by both McGie (1984) and Nickelson (1986), density-independent mortality is related to upwelling (U) and sea surface temperature (T), in the year of outmigration. For the sake of thoroughness, we include in our analysis the interaction term, UT, as well. Write, for Model 1,

(13) $A = \exp\{b_1 + b_2 U + b_3 T + b_4 UT\}$

The use of the exponential form assures the non-negativity of A. Correspondingly, for Model 2, we write,

(14) $C = \exp\{b_1 + b_2 U + b_3 T + b_4 UT\}$

The value of p^* lies between zero and one. This constraint is conveniently dealt with by writing

(15) $$p^* = \frac{\exp(b_5)}{1 + \exp(b_5)}$$

Form of the Statistical Error

Peterman (1981) discusses the alternatives of normal vs. log-normal error distribution. He presents evidence to support an assumption of the latter form, a matter duly addressed by subsequent authors. McCarl and Rettig (1983) go farther, acknowledging the possibility of more complex distributions, and dealing with the problem using the method of Just and Pope (1978, 1979). But there is more to the matter than simply describing a probability density. Let us examine the situation a bit further.

There are three components to statistical error. First, there are errors in the model's arguments (the so-called independent variables). Ideally, these variables are measured without error. With respect to the number of smolts, these errors are minimized when (as done here) smolts of only public hatchery fish are used. Second, there will be error about the dependent variable due to incompleteness of the model (upwelling, sea surface temperature, and smolt density alone do not completely determine survival). Finally, in our present case, run size, which we use to estimate survival, is a stochastic, not a deterministic, consequence of p, and therefore indicates p with error.

Point estimates of b-values obtained through statistical procedures depend, often dramatically, on assumptions about how the last two error terms described above are distributed (see, e.g. Schnute 1987). Unfortunately, the forms of these distributions are seldom known, although they can sometimes be approximated by returning to basic principles in model derivation (see the appendix).

To deal with the potential problems and biases arising from the above two considerations, we analyzed the OPIA coho salmon data, for both models, using two different statistical procedures, each based on very different assumptions about error structure.

In the first, we considered survival (p) to be a probability characteristic of individuals, and presumed the model to be complete. That is, individual-specific differences in viability can be ignored, and the influence of other, unmeasured, environmental variables can be assumed negligible. Statistical error, in this case, reflects binomial variability in adult run size about that expected on the basis of some annual, fixed p. The probability, given a particular model, of obtaining the run sizes observed, is thus

(16) $$L = \pi \binom{n_o}{n_R} p^{n_R}(1-p)^{n_o - n_R}$$

where n_o is the number of smolts released, n_R is the corresponding adult run size, p is survival as given in equation (12), and multiplication is over all years for which data are available. The values of the b's, A, D giving the largest L are the "most likely" values.

The second approach was to view p as a population characteristic (a proportion rather than a probability). Here the error term describes the year-to-year variation in p about that predicted by the models. The procedure is first to digress to the stochastic differential equations underlying the population dynamic process, in order to infer error structure. Once the

appropriate equations have been derived, non-linear regression can be performed. The calculations (see appendix for details and definitions) provide the following forms:

$$\text{(17a) Model 1: } \ln\left[\frac{n_R}{n_o}\frac{A + Bn_o}{Ap^* + Bn_R}\right] = -(\hat{\delta}_o\hat{\theta}) + \epsilon$$

$$\text{(17b) Model 2: } \ln(n_R/n_o) = \ln p^* - C(1 + Dn_o) + \epsilon$$

In both examples, if our basic assertion of normal, random error in δ_o is correct, ϵ is normally distributed with mean zero. The drawback to this approach is that we still do not know for sure if the error structure is valid. Hence, the assertion that $\epsilon \sim N(0, \sigma^2)$ cannot be defended rigorously. It is reassuring to note, however, that because $n_R \ll n_o$, $\ln\left[\frac{n_R}{n_o}\frac{A + Bn_o}{Ap^* + Bn_R}\right]$ is approximately $\ln(n_R/n_o) = \ln(p)$ when density-dependence B is weak. This accords with Peterman's (1981) evidence that survival is, in fact, approximately log-linearly distributed.

Analyses

As previously stated, our analyses are limited to public hatchery fish. Data used are shown in Table 1.

Before addressing the models directly, we computed a series of simple, partial regression coefficients, using log of survival to adulthood as the dependent variable (see Peterman 1981), and considering various combinations of physical variables (upwelling, sea surface temperature) and smolt densities as arguments. Although the more rigorous approaches below, reflecting both mechanism and a more thorough explanation of error structure are called for, this purely empirical approach (regression) is less obscure and may provide a more comfortable departure point for readers. Specifically, we wrote,

$$\text{(18) } \ln(p) = \beta_o + \beta_u U + \beta_t T + \beta_{ut} UT + \beta_w n_w + \beta_{pu} n_{pu} + \beta_{pr} n_{pr} + \epsilon,$$

where subscripts w, pu, and pr refer, respectively, to wild, public hatchery, and private hatchery smolts. The results of the partial regressions (Table 2) give only a hint that the survival of public hatchery fish, p, may be affected by smolts of their own kind. The evidence for an impact by wild fish is even less. However, the results do indicate a negative influence by private hatchery smolts.

Models 1 and 2

Our task now is to find values for b_1, b_2, b_3, b_4, b_5, and B (for Model 1), and b_1, b_2, b_3, b_4, b_5, and D (for Model 2) that best fit the data. The error structure appropriate for statistical analysis is derived in the appendix.

Non-linear relations such as those given in equations (16) and (17) often provide multiple solutions. On the preliminary belief, subsequently borne out in three of the four cases, that there would be a unique, biologically reasonable, non-trivial solution for each model and statistical approach, equations (17a) and (17b) were linearized (see appendix) to obtain a first crude estimate of the b's, B, and D. These estimates were then used in a multidimensional response surface search algorithm to obtain final solutions. In all cases, bootstrap procedures were then used to obtain 95% confidence ranges about the various coefficient estimates. Upwelling, temperature, and the interaction term affected survival; density-dependence was significant at the levels $P = 0.069$ (Model 1), $P = 0.055$ (Model 2), using the L_{max} statistical approach, but not significant in the one, non-trivial case using non-linear regression (Table 3).

Extension of the Models

Although arguments made above indicate little or no mixing of wild and hatchery smolts, there may, nevertheless, be indirect influences of one on another. Inclusion of wild and private hatchery smolts as influences on the survival of public hatchery smolts generates an intractable system of three simultaneous, stochastic, differential equations. We are, therefore, forced to

TABLE 2. Regression of log survival on various combinations of variables (regression coefficients ± 1 SE). U = upwelling index; T = sea surface temperature; n_w = number of wild smolts released; n_{pu} = number of public hatchery smolts released; n_{pr} = number of private hatchery smolts released.

Regression number	Arguments	Constant	U	T	UT	n_w	n_{pu}	n_{pr}	R^2
1	U	−4.34	0.216 ±0.046	—	—	—	—	—	0.477
2	T	3.58	—	−5.823 ±2.152	—	—	—	—	0.234
3	U, T	−1.60	0.187 ±0.053	−2.227 ±2.044	—	—	—	—	0.503
4	U, T, UT	−7.76	1.357 ±1.253	3.015 ±5.975	−1.002 ±1.073	—	—	—	0.522
5	U, T, UT, n_w	−8.26	1.405 ±1.273	3.285 ±6.071	−1.059 ±1.091	0.041 ±0.064	—	—	0.531
6	U, T, UT, n_{pu}	−7.72	1.289 ±1.245	3.242 ±5.933	−0.930 ±1.066	—	−0.013 ±0.011	—	0.550
7	U, T, UT, n_{pr}	−9.10	1.394 ±1.107	4.448 ±5.302	−1.063 ±0.947	—	−0.029	±0.011	0.644

TABLE 3. Results of analysis using Models 1 and 2 (derived coefficients with 95% confidence intervals).

Model 1	Model 2
$p = \dfrac{p^* e^{-\hat{\delta}_o \hat{t}}}{1 + \hat{\delta}\hat{t}\,(1 - e^{-\hat{\delta}_o \hat{t}})\, n_o}$	$p = p^* \exp\left\{-\mu\delta_o \left(1 + \dfrac{\mu'}{\mu}\, n_o\right)\right\}$
$: \hat{\delta}_o \hat{t} = \exp\{b_1 + b_2 U + b_3 T + b_4 UT\}$	$: \mu\hat{\delta} = \exp\{b_1 + b_2 U + b_3 T + b_4 UT\}$
L_{max} approach	
$p^* = 0.510$	$p^* = 0.257$
$b_1 = 5.176$	$b_1 = 4.518$
$b_2 = -0.01186 \pm 0.00047$ ($P<0.0001$)	$b_2 = 0.01105 \pm 0.00056$ ($P<0.0001$)
$b_3 = -0.03369 \pm 0.0749$ ($P<0.0001$)	$b_3 = -0.03141 \pm 0.02119$ ($p<0.05$)
$b_4 = 0.00930 \pm 0.00223$ ($P<0.0005$)	$b_4 = 0.00861 \pm 0.00032$ ($P<0.0001$)
$\delta t = 0.0435 \pm 0.0486$ ($P=0.069$)	$\mu'/\mu = 0.0102 \pm 0.0120$ ($P=0.055$)
R^2 (around non[linear regression model) = 0.866	R^2 (around non-linear regression model) = 0.995
R^2 (around run size) = 0.625	R^2 (around run size) = 0.635
Non-linear regression	
No non-trivial solution	$p^* = 0.304$
	$b_1 = 4.519$
	$b_2 = -0.01033 \pm 0.00028$ ($p<0.0001$)
	$b_3 = -0.02960 \pm 0.01968$ ($p<0.005$)
	$b_4 = 0.00802 \pm 0.00016$ ($p<0.0001$)
	$\mu'/\mu = 0.0059 \pm 0.0157$ (NS)
	R^2 (around non-linear regression model) = 0.995
	R^2 (around run size) = 0.637

simplify our formulations. Suppose that mortality rates of the three stock components are in a constant proportional relation during the critical period of (potential) interaction. Then, let i, j denote the component stocks, $\delta_j = q_{ij}\delta_i$, where q_{ij} is a proportionality constant, $n_j = z_{ij}n_i$, where z_{ij} is n_j/n_i at sea entry, and

$$(19) \quad -\frac{1}{n_i}\frac{dn_i}{dt} = \delta_{io} + \delta_i n_i + \sum_{j \neq i}(\delta_i q_{ij}) m_{ij}\alpha_{ij}(z_{ij}n_i)$$

Here, m_{ij} is a mixing coefficient and α_{ij} is the competition coefficient, both of which are presumed constant year-to-year.

Now the previous analyses indicate that density-dependent feedback, if it occurs, is slight. Therefore, the approximate solution given in the appendix (equation $(A-4)$) is appropriate, and we can write

$$\begin{aligned}\ln(p_i) &\simeq \ln(p_i^*) - (\hat{\delta}_{io}\hat{t}) - (\delta_i\hat{t})\,(n_{io}/\hat{\delta}_{io}\hat{t}) \\ &\quad - \sum_{j \neq i}(\delta_i \hat{t} q_{ij} m_{ij}\alpha_{ij})\,(z_{ij}n_{io}/\hat{\delta}_{io}\hat{t}) + \epsilon \\ &= \ln(p_i^*) - (\hat{\delta}_{io}\hat{t}) - (\delta_i\hat{t})\,(n_{io}/\hat{\delta}_{io}\hat{t}) \\ &\quad - \sum_{j \neq i}(\delta_i \hat{t} q_{ij} m_{ij}\alpha_{ij})\,(n_{jo}/\hat{\delta}_{io}\hat{t}) + \epsilon\end{aligned}$$

$$(20) \quad : \epsilon \sim N(0, \sigma^2 t)$$

(The reseparation of n_j's is valid only under the assumption that $q_{ij}m_{ij}\alpha_{ij}$ is invariant year-to-year.)

Equation (20) must be considered crude because of the simplifications and assumptions necessitated by the complexity of the problem. The equation provides a rationale for further analysis, but a full, non-linear treatment is not warranted. A much simpler treatment is possible if we write $\hat{\delta}_{io}\hat{t}$ as we wrote A in equation (13), and assume values for b_1, b_2, b_3, and b_4. Because the confidence intervals on these b coefficients (for U, T, UT) are extremely tight under the preceding analysis, we used these, and calculated year-to-year values for $(\hat{\delta}_{io}\hat{t})$, $n_{io}/\hat{\delta}_{io}\hat{t}$, and $n_{jo}/\hat{\delta}_{io}\hat{t}$; and then performed a partial linear regression (equation (20)). Only private hatchery fish affected the survival of public hatchery fish at a statistically significant level (Table 4).

Discussion and Conclusions

What are we to conclude? First, any tendency for fishery biologists to take Nickelson (1986) as the final word, concluding no density-dependence at sea, is at best premature. Indeed, if our assertion of little or no mixing of private and public hatchery and wild fish is valid, and if statistical error reflects largely binomial capriciousness as opposed to incompleteness of the model, then the evidence supports the existence of density-dependence. This is true for both models. That is, it is true under either of two, underlying, biological assumptions: density-dependence, if it occurs, works via an effect on mortality; density-dependence, if it occurs, works via an effect on growth rate. However, if statistical error reflects largely a failure of the model to account for environmental vagaries, the conclusion is considerably weakened (not statistically significant). Inasmuch as these results are based on models derived explicitly with the density-dependence question in mind, and from biological first principles, they should be considered more reliable than previous conclusions based on empirical models.

If we accept the conclusion of no mixing, how are we to account for the apparent impact of private hatchery fish, indicated both in the simple regression and in the extended model? Might the density effects indicated in analysis of the two models be an artifact related to the correlation over time of private and public hatchery smolt densities? This seems unlikely; the correlation coefficient calculated from data in Table 1 is only 0.387. We can only speculate about the impact of the private hatchery fish. Perhaps, even though mixing seems to occur only on a large spatial scale, the sudden and massive influx of private

TABLE 4. Regression coefficients ± 1SE.

Model from which values for b_1, b_2, b_3, and b_4 are taken	ln (p^*)	Density effect of smolts: Wild	Density effect of smolts: Public hatchery	Density effect of smolts: Private hatchery	R^2
Model 1, L_{max}	−0.773	0.039 ±0.076	0.010 ±0.017	0.061 ±0.026	0.261
Model 2, L_{max}	−1.550	0.020 ±0.032	−0.001 ±0.007	0.020 ±0.008	0.212
Model 2, Non-linear regression	−1.360	0.007 ±0.027	−0.002 ±0.005	0.015 ±0.007	0.238

hatchery smolts into the nearshore area induces search images in nearshore predators, both piscine and avian, for juvenile coho salmon, incuding yearling public hatchery and wild smolts. This would lead to increased predation on the wild smolts in years of high private hatchery releases.

In summary, the evidence suggests that coho salmon smolts interact in the nearshore area in a way that generates density feedback on survival. Though this evidence is not strong, statistically, the prevailing view of no density-dependence should be strongly discouraged. For those who insist on a type I error lying below 0.05, or who argue a weaker conclusion on the basis that much of the statistical error reflects weaknesses in the biological models, we point out that failure to reject a null hypothesis is *not* equivalent to accepting it (Peterman 1989).

If density-dependent mortality occurs at sea, increased production of hatchery fish will not result in proportional increases in total production. The economic implications would seem to merit directed, large-scale experiments, similar to those proposed by Walters (1989), to test for the degree of density-dependent mortality. At the very least, the current assumption, that density-dependence does not occur, based on Nickelson's (1986) analysis, should remain open to question.

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Appendix

For Model 1, consider equation (3),

$$\frac{1}{n}\frac{dn}{d\theta} = -\delta_o - \delta n,$$

and define $x = \ln(1 + \frac{\delta_o}{\delta n})$. Then

$$dx = \left[-\frac{1}{1 + \frac{\delta_o}{\delta n}} \right] \left[\frac{\delta_o}{\delta n^2} \right] dn = -\frac{1}{n}\frac{dn}{1 + \frac{\delta n}{\delta_o}},$$

and so,

$$\frac{1}{n}\frac{dn}{d\theta}\left[= -\delta_o - \delta n = -\delta_o(1 + \frac{\delta_o}{\delta n}) \right] = \frac{dx}{d\theta}(1 + \frac{\delta n}{\delta_o}).$$

Therefore,

$$\text{(A-1)} \quad \frac{dx}{d\theta} = \delta_o .$$

Now δ_o is constrained to be non-negative. Therefore, stochastic variation in δ_o can likely be approximated with the log-normal distribution. That is, we can write,

$$\text{(A-2)} \quad \delta_o = \hat{\delta}_o e^{\sigma' W(\theta)}$$

Because density-dependent mortality is presumably minor compared with density-independent mortality (if not, the exercise in this paper would be unnecessary), survival is reasonably approximated with equation (5)

$$p^* e^{-\delta_o \hat{\theta}}$$

Variation in log(survival), then, equals

$$\text{Var}\,(\delta_o\hat{\theta}) = (\hat{\delta}_o\hat{\theta})^2\,\text{Var}(\delta_o) = (\hat{\delta}_o\hat{\theta})^2\sigma'^2\,.$$

Therefore,

$$\text{(A-3)}\quad \frac{\text{Var}\,(p)}{(\hat{\delta}_o\hat{\theta})^2} = \frac{\text{Var}\,(p)}{(\ln\bar{p})^2} = \sigma'^2$$

Examination of the data in Table 1 now tells us that

$$\sigma'^2 = \frac{\text{Var}\,(p)}{(\ln\bar{p})^2} = 0.00006\,,$$

whence,

$$\delta_o = \hat{\delta}_o e^{\sigma' W(\theta)} \longrightarrow \hat{\delta}_o(1 + \sigma' W(\theta)).$$

Therefore, because Var $(p)/(\hat{\delta}_o\hat{\theta})^2$ is so small, a normal approximation is justified, and we can write,

$$\text{(A-4)}\quad \frac{dx}{dt} \longrightarrow \hat{\delta}_o + \hat{\delta}_o\sigma' W(\theta) \equiv \hat{\delta}_o + \sigma W(\theta)$$

The solution to (A-4) is

$$x(\theta) \sim N(x_o + \hat{\delta}_o\hat{\theta},\, \sigma^2\hat{\theta}).$$

Substituting for x, then, and setting $(\hat{\delta}_o\hat{\theta}) = A$,

$$\text{(A-5)}\quad \ln\left[\frac{n(\hat{\theta})}{n_o}\frac{A + Bn_o}{A + Bn(\hat{\theta})}\right] = \ln\left[\frac{n_R}{n_o}\frac{A + Bn_o}{p^*A + Bn_R}\right] \sim N(-A, \sigma^2\hat{\theta})$$

Continuing with the conservative assumption that density-dependent mortality is slight compared with density-independent mortality, equation (A-5) can be closely approximated with

$$\ln\left[\frac{n_R}{n_o}\left(1 + \frac{Bn_o}{A}\right)\right] - \ln p^* = \ln\left(\frac{n_R}{n_o}\right) + \ln\left(1 + \frac{Bn_o}{A}\right) - \ln p^*$$

$$\simeq \ln\frac{n_R}{n_o} + \frac{B}{A}n_o - \ln p^* \sim N(-A, \sigma^2\hat{\theta})\,.$$

Thus,

$$\text{(A-6)}\quad \ln(p) = \ln\left(\frac{n_R}{n_o}\right) \sim N(\ln p^* - A - \frac{B}{A}n_o, \sigma^2\hat{\theta})\,.$$

Now approximate B/A by the constant b, recall (equation (13)) that $A = \exp\{b_1 + b_2U + b_3T + b_4UT\}$, and note that because B lies roughly between 2 and 3 (providing a density-independent survival between about 0.05 and 0.14), the bracketed expression is close to 1.0. Therefore,

$$\ln p \simeq \ln p^* - (1 + b_1) - b_2U - b_3T - b_4UT - bn_o + \epsilon,\ :\ e \sim N(0,\sigma^2\hat{\theta})$$

providing us a simple, linear form for regression. The outcome, providing a first estimate for a solution (with standard errors), is

$1 + b_1 - \ln p^* = 7.720$
$b_2 = -0.01289 \pm 0.01245$
$b_3 = -0.03242 \pm 0.05933$
$b_4 = 0.00930 \pm 0.01066$
$b = 0.013 \pm 0.011$, implying that B lies in the vicinity of 0.04 to 0.05. These results (using $B = 0.045$) and trial values of p^* ranging from 0.3 to 1.0, were next used as input to a routine used to find values yielding maximum likelihood. Confidence intervals for the b-values were calculated with the bootstrap technique. Output from the L_{max} calculations was used as input for the non-linear regressions.

With respect to Model 2, we suppose that δ_o varies as $\hat{\delta}_o + w(t)$, and write

$$\text{(A-5)}\quad \frac{1}{n}\frac{dn}{dt} = -\hat{\delta}_o + w(t),$$

from which (equation (12))

$$\text{(A-6)}\quad \ln(p) \sim N(\ln p^* - C(1 + Dn_o), \sigma^2\hat{t}).$$

Then setting

$$C = \exp\{b_1 + b_2U + b_3T + b_4UT\} \simeq 1 + b_1 + b_2U + b_3T + b_4UT$$

and approximating CD by the constant b_5, we may, as before, find initial values for the b's by regressing $\ln(p)$ on U, T, UT, and n_o.

Occurrence, Relative Abundance, and Size of Landlocked Sea Lamprey (*Petromyzon marinus*) Ammocoetes in Relation to Stream Characteristics in the Great Lakes

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The effect of 14 environmental variables on the occurrence of sea lamprey (*Petromyzon marinus*) ammocoetes was examined in 73 tributaries of the Great Lakes. We successfully classified 86% of streams without lamprey and 90.5% of streams with ammocoete populations using discriminant analysis. Eighty percent of streams in a test data set were also successfully classified. The classification success was largely determined by differences in stream substrate characteristics based on the magnitude of canonical coefficients and contribution to the multivariate *F*-statistic. Streams with ammocoetes had significantly ($P<0.10$) higher proportion of sand and a lower proportion of bedrock and clay than streams without ammocoetes. Catch per unit effort (CPUE) of ammocoetes collected with electro-fishing gear was also significantly related ($P=0.004$) to the proportion of rubble, gravel, and clay. As well, we observed a significant ($P<0.01$) positive relationship between conductivity and temperature with size of 2^+ ammocoetes. Results indicate that it should be possible to develop predictions for the number of metamorphosing ammocoetes based upon differences in stream characteristics.

Des analyses corrélationnelles considérant, d'une part, 14 variables environnementales et, d'autre part, la présence ou l'absence de lamproies marines (*Petromyzon marinus*) dans 73 affluents des Grands Lacs ont été effectuées. Au moyen de l'analyse discriminante, nous avons réussi à caractériser 86% des cours d'eau dépourvus de lamproies et 90.5% des cours d'eau abritant des populations d'ammocètes. Nous avons aussi réussi à classer 80% des cours d'eau dans un ensemble de données d'essai. La capacité de classer les cours d'eau dépendait largement des différences dans les caractéristiques du substrat établies suivant la valeur des coefficients canoniques et la contribution de ces variables à la statistique multivariée *F*. Les cours d'eau abritant des ammocètes avaient des proportions de sable et de substrat rocheux significativement ($P<0,10$) plus et moins importantes, respectivement, par rapport aux cours d'eau dépourvus d'ammocètes. Les prises d'ammocètes par unité d'effort effectuées à l'électricité étaient aussi significativement ($P=0,004$) corrélées aux proportions de moellon, de gravier et d'argile. De plus, il y avait une corrélation positive significative ($P<0.01$) entre la température et la conductivité, d'une part, et la taille des ammocètes d'âge 2^+. Nos résultats montrent qu'il serait possible de prédire les quantités d'ammocètes en métamorphose dans les cours d'eau d'après les caractéristiques propres à ces derniers.

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The sea lamprey (*Petromyzon marinus*) is of considerable economic importance to the Great Lakes because it parasitizes salmonids and other game species resulting in significant mortality (Smith and Tibbles 1980; Moore and Lychwick 1980). The Great Lakes fishery is an important natural resource and has been valued at over $1.4 billion (Talhelm 1988). Resource managers are concerned that, despite current control measures, sea lamprey contribute to salmonid mortality (Pycha 1980; Bergstedt and Schneider 1988) such that a significant proportion of the fish that otherwise would be available to sport and commercial exploitation are removed. At present, lamprey populations are controlled primarily by killing their ammocoetes (i..e the immature, stream-resident, life stage) before metamorphosis to the juvenile, parasitic phase (lake-resident). Chemical control is achieved through the application of the larvicide, 3-trifluromethyl-4-nitrophenol (TFM) to Great Lake tributaries with resident ammocoete populations (Torblaa and Westman 1980).

Sea lamprey have readily adapted to the Great Lakes from the anadromous form of the species common to the Atlantic Ocean. However, sea lamprey ammocoetes have been reported from less than 7.5% of Great Lakes tributaries (Morman et al. 1980) despite the widespread distribution of adults throughout the lakes. Hardisty and Potter (1971), Potter (1980), and Morman et al. (1980) have shown that, within a stream, distribution of ammocoetes is largely determined by the availability of burrowing habitat, ambient water quality and physical barriers to spawning sea lamprey. Morman et al. (1980) and Purvis (1979)

TABLE 1. Treatment means of stream characteristics (variables from 73 streams in 5 Great Lakes) used in discriminant analysis.

Variable	Absent	Present
Bedrock (%)	7.13	0.88
Rubble (%)	11.53	6.69
Gravel (%)	12.65	16.05
Sand (%)	29.53	39.75
Silt (%)	23.39	24.40
Clay (%)	15.45	10.23
Discharge (m^3/s)	6.45	40.11
Temp (°C)	11.08	10.46
Alkalinity (mg/L)	159.11	125.58
Conductivity (μS/m at 25°C)	571.22	339.03
Dissolved O_2 (mg/L)	10.13	10.45
Total P (mg/L)	0.12	0.06
Seston (mg/L)	42.34	26.01
Turbitity (FTU)	21.05	11.45

have shown that density and metamorphosis vary considerably among streams in the Great Lakes. As well, Potter (1980) has reported that the onset of metamorphosis is dependent on size and growth of ammocoetes. While we know that only 433 streams produce sea lamprey ammocoetes and that considerable differences exist in abundance and transformation rates, the environmental factors that cause these differences among streams in the Great Lakes Basin have not been identified. Consequently, we first determined if the distribution (presence/absence) of sea lamprey ammocoetes among Great Lakes tributaries could be described as a function of physical and chemical habitat variables using classification analysis. Next, we examined the relationship between a surrogate of abundance (catch per unit effort — CPUE) and growth (size of ammocoetes at age 2^+) with physical and chemical habitat variables of streams from L. Superior to L. Ontario.

Materials and Methods

Presence/absence of ammocoetes in Great Lakes tributaries

Data from streams historically surveyed by the Sea Lamprey Control Centres of the Great Lakes Fishery Commission (GLFC) were used to determine if physical/chemical characteristics of streams could be used to classify streams as suitable for sea lamprey ammocoetes. We selected 73 tributaries of Lakes Superior, Michigan, Huron, Erie, and Ontario that had been previously surveyed for lamprey presence, substrate composition, and water chemistry (Table 1). Streams with obvious barriers to spawning sea lamprey (i.e streams that dried up in summer or had dams or waterfalls that prevented spawning migrations) were excluded from this analysis.

Lamprey survey crews visually classified the stream bottom composition at each sampling station. Six substrate classes were used in streams found along the Canadian and New York shores and seven classes along the remaining U.S. shoreline. We arbitrarily combined two classes, "boulder" and "rubble" from U.S. data in order to harmonize the two data sets (Table 1). The average of each substrate class was calculated from all stations in a stream. Data from one to three surveys were averaged to obtain values for stream bottom composition because streams frequently treated with TFM (3–5 y treatment rotation) were regularly surveyed between chemical treatments and untreated streams were surveyed less frequently. Survey stations were not randomly selected by the survey crews but were areas which historically supported sea lamprey ammocoetes. Therefore, the stations used were biased towards stream sections perceived as "optimal" ammocoete habitat.

Discharge data were obtained from published annual reports of Water Survey of Canada (WSC 1983, 1984, 1986), the U.S. Geological Survey (USGS 1985, 1986, 1987) and the Ontario Ministry of the Environment (OMOE) stream water quality survey. The yearly average of approximately monthly water chemistry samples was calculated for each stream.

Statistical analyses were performed using a micro-computer version of Systat 4.0 (Wilkinson 1988). Discriminant analysis (Bock 1975) was used to determine the ability of the 14 physical and chemical stream characteristics (descriptor variables) to classify streams as to whether ammocoetes were present or absent (grouping variable). Prior to analysis, the data set was randomly separated into a calibration data set (63 streams) and a test data set (10 streams). The canonical variate was calculated using the calibration data set and its predictive ability assessed with the test data set.

Relative Abundance of Ammocoetes

Streams with known sea lamprey populations are regularly sampled using electro-fishing gear to determine distribution and population structure within streams. We calculated the CPUE as the number of ammocoetes collected per person hour of effort from 16 Canadian tributaries of Lakes Superior, Huron, and Ontario. Mean log CPUE was calculated as the average CPUE from two to 10 sampling stations on each stream. We used step-wise regression to develop models to estimate mean log CPUE for each stream from our suite of environmental variables. Residuals were examined for deviations from regression model assumptions. Because electro-fishing for ammocoetes was designed to establish distribution, bias may result from using this data to reflect abundance. However, no alternative exists to compare differences in abundance among streams.

Size of Ammocoetes at Age 2^+

We used regression analysis to examine the relationship between physical and chemical variables and ammocoete size. We selected 17 streams that had both environmental data and relatively large collections of ammocoetes. Year-classes were assigned using a maximum likelihood method (Mix 2.3) to analyse length frequency distributions (see MacDonald and Pitcher 1979; MacDonald 1987). We then estimated the mean length of year-class (YC) 2^+ ammocoetes. No attempt was made to verify ages by analyzing statolith banding (Beamish and Medland 1988). However, we were confident in the aging technique because we knew the number of years between chemical treatments and we assumed a low survival rate following these treatments. We did not consider young-of-the-year because they are small, difficult to collect, and are poorly represented in most samples. Older year-classes were excluded because the degree of overlap between length frequency distributions was such that individual year-classes could not be reliably separated.

Step-wise regression was used to assess the physical or chemical variables most important in determining differences in ammocoete length between streams. Residuals of the regression analysis were examined to assess deviations from regression analysis assumptions.

Results

Presence/Absence of Ammocoetes in Great Lakes Tributaries

The classification success of the discriminant analysis model for the calibration data set was 86% for streams without lamprey

TABLE 2. Classification of streams for the presence or absence of sea lamprey ammocoetes as determined by discriminant analysis using data from (A) the calibration data set and (B) the test data set.

A. Calibration data set

	Predicted		
Group	Absent	Present	Total
Absent	18	3	21
Present	4	38	42
Total	22	41	63

B. Test data

	Predicted		
Group	Absent	Present	Total
Absent	4	1	5
Present	1	4	5
Total	5	5	10

and 90.5% for streams with lamprey (Table 2a). Eight of ten streams in the test data were correctly classified by the canonical variate (Table 2b) with similar classification success among the present and absent groups. The multivariate test statistic (Wilks Lambda) was significant ($F = 3.602$; df = 14, 48; $P < 0.001$), indicating that the classification success was not spurious.

The magnitude of the standardized canonical coefficients (absolute value) are generally used to determine the relative importance of descriptor variables used in discriminant analysis (Legendre and Legendre 1983). However, the stability of these coefficients and the ease of interpretation is reduced when there is a high degree of correlation among the descriptor variables (Bock 1975; Campbell and Atchley 1981). In our data set, there was considerable correlation among the 14 variables used to classify lamprey streams (Bartlett chi-square = 583.31, df = 91, $P < 0.001$). Examination of the significant correlation coefficients (Bonferroni adjusted probabilities) suggested correlation among the substrate size variables and discharge, productivity related variables (i.e. alkalinity, conductivity, and total phosphorus) and between turbidity and suspended sediments.

Wilkinson (1975) outlines four criteria for determining the importance of variables in canonical variate analysis:

i) the magnitude of the univariate *F*-tests,
ii) the magnitude of the standardized canonical coefficients,
iii) the contribution of each variable to the multivariate *F*-statistic, and
iv) multivariate and univariate confidence intervals for linear contrasts between groups.

In our study, (iv) reduces to the significance of the *t*-test or ANOVA because we had only 1 *DF* for groups.

Table 3 contrasts the relative importance of the stream characteristics using these four criteria. In the univariate case, 10 of the 14 variables were significantly different between streams with and without sea lamprey ammocoetes. Total phosphorus, conductivity, and bedrock had the largest univariate *F*-statistics. When viewed univariately, these three stream attributes are the most valid response variables (Wilkinson 1975). However, bedrock, sand, and clay had the greatest standardized canonical coefficients indicating that they contributed most to the discrimination between streams with and without ammocoetes. Finally, bedrock had the largest reduction in the multivariate *F*-statistic which further supports the importance of substrate variables in the classification of streams.

The interpretation of the discriminant analysis was complicated by the extent of correlation among the stream characteristics. Ammocoetes are clearly less likely to occur in streams with larger average substrate size than in streams with smaller average particle size (Fig. 1). Our analysis indicates the presence/absence of sea lamprey ammocoetes within the Great Lakes is controlled, to a large degree, by substrate particle size.

Relative Abundance

The average CPUE among the 16 streams used in this study ranged from <0.1 ammocoetes·h^{-1} to 180 ammocoetes·h^{-1}. The step-wise regression between CPUE and relative abundance retained rubble, gravel, clay, and total phosphorus. These variables were significantly related to CPUE ($R^2 = 0.65$, $P = 0.004$) and were defined by the equation:

(1) log CPUE = 3.89 − 0.66*rubble + 0.49*gravel − 1.59*clay

Rubble and gravel had the largest standardized coefficients which indicates that they were the most important variables in the regression (Table 4). In addition, the coefficients of these variables were negative which indicates that the low relative abundance occurred in streams with a higher proportion of difficult burrowing habitat like rubble and clay. On the other hand, gravel had a positive relation to relative abundance. This suggests that streams with higher relative abundance of ammocoetes had a larger proportion of gravel.

Size of Ammocoetes at Age 2$^+$

The average length of YC 2$^+$ ammocoetes in the 17 streams ranged from 57 mm to 126 mm. Of the 14 stream characteristics used to explain the variation in ammocoete lengths, only conductivity and temperature were retained by step-wise multiple regression. Ammocoete length was related to temperature and conductivity ($n = 17$, $R^2 = 0.83$, $P < 0.001$) and was defined by the equation:

(2) Length = 31.70 + (0.09* Conductivity) + (2.60* Temperature)

Conductivity had a larger standardized regression coefficient than temperature (Table 5). Therefore, we concluded that conductivity was more important in explaining between-stream differences in ammocoete length. As stream conductivity increased, the length of 2$^+$ ammocoetes also increased (Fig. 2). Conductivity in the linear regression model explained 69% of variation in ammocoete length.

Discussion

Only 433 of the 5 747 tributaries of the Great Lakes have collection records for sea lamprey ammocoetes (Morman et al. 1980). In our data set, streams without ammocoetes had larger average substrate particle size and, apparently, an insufficient proportion of sand–silt habitat to maintain an ammocoete population, given current populations of parasitic-phase lamprey. Conversely, streams with sea lamprey ammocoetes had lower

TABLE 3. Univariate *F*-statistics, standardized canonical coefficients, canonical loadings, and contributions to the multi-variate *F*-statistic for stream characteristics used in discriminant analysis.

Variable	*F*-ratio	St. Coeff	Loading	MV-F
Bedrock	9.408	1.390	0.383	3.082
Rubble	3.492	0.804	0.233	3.780
Gravel	1.029	0.340	−0.127	3.934
Sand	4.063	1.572	−0.252	3.762
Silt	0.088	0.611	−0.037	3.879
Clay	4.848	1.281	0.275	3.412
Discharge	6.513	−0.399	−0.319	3.517
Temp	0.983	0.039	0.124	3.956
Alkalinity	2.852	−0.197	0.211	3.897
Conductivity	11.075	0.865	0.416	3.266
Dissolved O_2	1.440	0.041	−0.150	3.955
Total P	11.089	0.221	0.416	3.905
Seston	3.509	−0.943	0.234	3.183
Turbidity	3.905	0.300	0.247	3.837

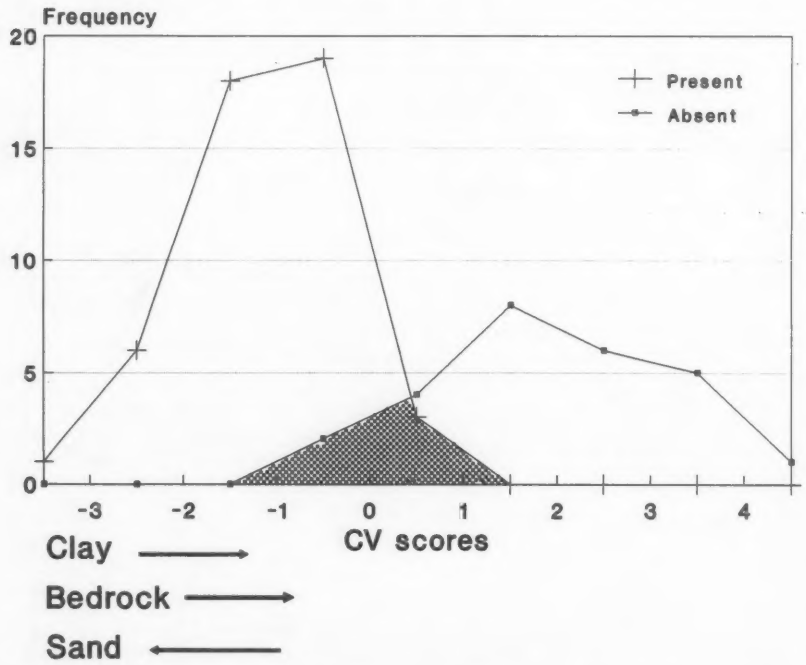

FIG. 1. Frequency polygon of canonical variate scores from 63 streams with and without sea lamprey ammocoetes. The stippled area represents the region of misclassification. The arrows represent the correlation between important discriminating variables and the canonical variate.

TABLE 4. Regression coefficients, standardized coefficients of stream characteristics retained by step-wise regression of CPUE and the habitat.

Variable	Coefficient	SE	Standardized coefficient	*P*
Constant	3.89	1.01	0.00	0.00
Rubble	−0.66	0.27	−0.45	0.03
Gravel	0.49	0.23	0.42	0.05
Clay	−1.59	0.60	−0.49	0.02

TABLE 5. Regression coefficients, standardized coefficients and prob. of variables retained by step-wise regression of size of 2^+ ammocoetes and habitat variables.

Variable	Coefficient	SE	Standardized coefficient	*P*
Constant	31.70	13.06	0.00	0.029
Conductivity	0.09	0.01	0.83	0.001
Temperature	2.59	1.37	0.21	0.080

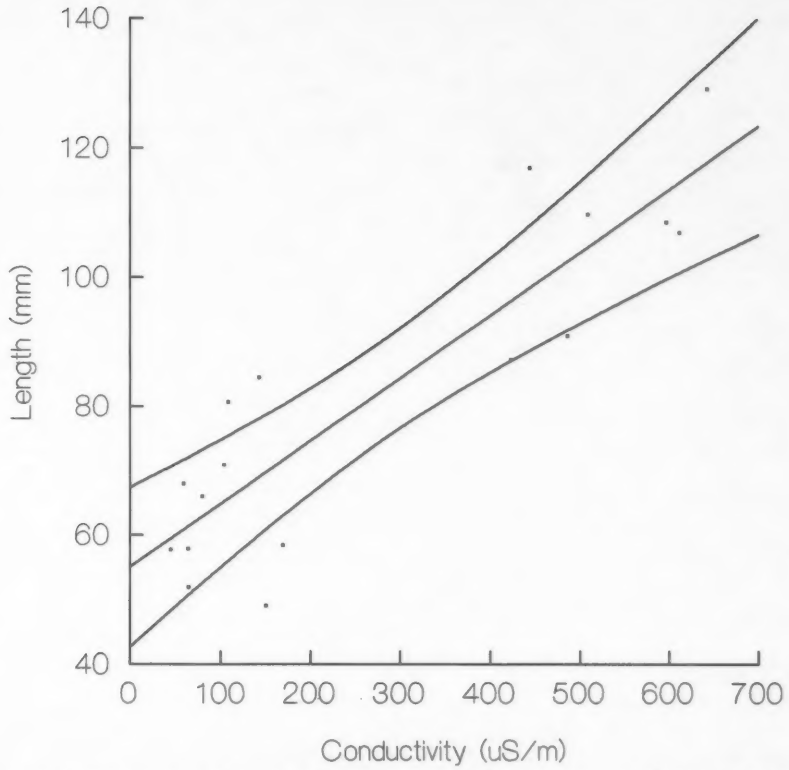

FIG. 2. Linear regression of stream conductivity and length of 2^+ ammocoetes with 95% confidence bands.

proportions of bedrock and rubble and higher proportions of sand substrate. Our results are the first to suggest that availability of optimal stream substrate size may be an important factor limiting the distribution of landlocked sea lamprey ammocoetes within the Great Lakes. Further, our conclusions are similar to previous studies that have cited substrate particle size as an important variable influencing the occurrence and abundance of ammocoetes of several species of lamprey within a stream (Thomas 1962; Hardisty and Potter 1971; Malmquist 1980; Potter et al. 1986). We have also demonstrated a significant relationship between substrate conditions and relative abundance (CPUE) of ammocoetes from 16 streams used in this analysis. While we have concern about the validity of the CPUE data, the general relationship between the quality of burrowing habitat and ammocoete abundance is logical in light of the factors that determine presence/absence of ammocoetes.

The link between ammocoete population densities and stream habitat could enable the development of predictive relationships for abundances of ammocoete populations akin to the morphoedaphic index for fish yield (Ryder 1982). Relationships such as those developed here could permit the estimation of sea lamprey ammocoete populations in a lake-wide perspective. Variables other than substrate size, such as water depth, current velocity, and the concentration of organic material in the substrate have been identified (Potter et al. 1986; Malmquist 1980) as important factors influencing the abundance of ammocoetes. Quantitative assessment of any of these variables in all tributary systems of the Great Lakes with lamprey populations would be prohibitively expensive. However, many stream characteristics are similar in that most are a function of stream channel gradient and local geology (Baxter 1957; Hardisty & Potter 1971; Malmquist 1980). Gradient will determine the depositional and erosional areas, water depth, and velocity while local geology will influence the origin and size of particles in the stream. The simplest method of developing predictive relationships for ammocoete populations might result from using gradient profiles as a "surrogate variable" for the suite of environmental variables now used to describe optimal ammocoete habitat.

Our results also indicate that conductivity and temperature were significantly related to ammocoete size, and by extension, growth in established stream populations. Streams with higher conductivity (hardwater streams) were associated with larger 2^+ ammocoetes. Lamprey ammocoetes feed by filtering algae and detritus (Hardisty and Potter 1971). In general, hardwater streams have greater primary production than softwater streams (Ryder 1965; Ryder and Pesendorfer 1988; Hynes 1970). As well, conductivity was correlated with total P and alkalinity in our data set. Therefore, the amount of food available to lamprey should be greater in hardwater streams and should result in faster growth rates. We also found larger ammocoetes in streams with higher average temperatures, which we would generally expect from poikilotherms operating within their thermal tolerances. Our results confirm that growth of ammocoetes in Great Lakes tributaries are at least in part influenced by temperature (Purvis 1979; Purvis 1980). Because faster growing ammocoetes metamorphose to the parasitic phase more quickly (Potter 1980),

differences in conductivity and temperature are likely to influence growth and metamorphosis of ammocoetes throughout the Great Lakes.

We submit that our results be accepted with caution largely because several critical variables (CPUE, substrate variables) were measured semi-quantitatively. Nevertheless, it is evident that differences in substrate among streams are important in determining first, whether streams are colonized by sea lamprey and second, the relative abundance of ammocoetes. In established populations, the size of 2^+ ammocoetes was related to temperature and conductivity. Thus, production of ammocoetes among streams can be modelled using few environmental attributes. Accurate predictions of the number of metamorphosing ammocoetes entering the Great Lakes will be a critical element in future attempts at modelling the sea lamprey — salmonid interactions under varying sea lamprey control strategies.

Acknowledgements

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Interactions between White Perch (*Morone americana*) and Yellow Perch (*Perca flavescens*) in Lake Erie as Determined from Feeding and Growth

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Parrish, D. L., and F. J. Margraf. 1990. Interactions between white perch (*Morone americana*) and yellow perch (*Perca flavescens*) in Lake Erie as determined from feeding and growth. Can. J. Fish. Aquat Sci. 47:1779–1787.

Since the mid-1970's, white perch *Morone americana* have expanded rapidly, resulting in possible major interactions with the native yellow perch *Perca flavescens*. We compared the food consumption rates, diet overlap, and growth of white perch and yellow perch from field data collected during 1983–85 and 1987. Food consumption rates were as much as 27% greater in white perch than in yellow perch, and were higher for both species in the central basin than in the western basin. Seasonal diet composition was most alike in summer and less so in spring and fall, when yellow perch ate more benthos or fish than did white perch. Of 48 Schoener index comparisons of diet overlap during a 3-yr period, 52% were significant (>0.6). Although yellow perch grew faster in the central basin, reflecting the greater consumption rates, white perch did not show the similar large interbasin growth differences.

Depuis le milieu des années 1970, le bar-perche *Morone americana* s'est étendu rapidement, entraînant d'importantes interactions possibles avec la perchaude indigène *Perca flavescens*. Nous avons comparé le taux de consommation des aliments, le chevauchement du régime alimentaire et la croissance du bar-perche et de la perchaude à partir de données sur le terrain recueillies entre 1983–85 et en 1987. Le taux de consommation des aliments était jusqu'à 27% plus élevé chez le bar-perche que chez la perchaude, et chez les deux espèces, il était plus élevé dans le bassin central que dans la partie ouest du bassin. La composition saisonnière du régime alimentaire était à peu près semblable en été et un peu moins au printemps et à l'automne lorsque la perchaude se nourrissait davantage de benthos ou de poisson que le bar-perche. Sur les 48 comparaisons de l'indice Schoener du chevauchement du régime alimentaire pendant une période de trois ans, 52% étaient significatives (>0,6). Même si la perchaude se développait plus rapidement dans le bassin central, ce qui traduit des taux de consommation plus grands, le bar-perche ne présentait pas les mêmes différences importantes de croissance entre les bassins.

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White perch, *Morone americana*, an East Coast estuarine fish, were first collected in Lake Erie in 1953 (Larsen 1954), but did not proliferate until the mid-1970's. In the early 1980's, both numbers of young-of-the-year and commercial catches increased greatly (Boileau 1985; Ohio Department of Natural Resources 1985). Schaeffer (1984) and Schaeffer and Margraf (1986a, b) concluded that interactions between white perch and yellow perch, *Perca flavescens*, in Lake Erie may result in competition. However, they fell short of showing that white perch interacted negatively with yellow perch because collecting sites and times for the two species did not overlap, and sampling was restricted to the Sandusky Bay area of western Lake Erie.

Hartman et al. (1980) indicated that yellow perch growth rates were similar in the central and western basins of Lake Erie through the 1960's. According to Hayward and Margraf (1987), even though yellow perch growth rates have declined for 15 y in the western basin and for the last few years in the central basin, a more rapid decline has occurred since the white perch invasion. Yellow perch growth rates have declined even more in the more food-limited western basin than in the central basin (Hayward and Margraf 1987).

Hanson and Leggett (1986) and Werner (1986) described several conditions, especially related to fish communities, which indicate the occurrence of competitive interactions. For example, if the individual growth rates of an indigenous species decline after the invasion of a new species and both species use the same food-limiting resource, then competition has presumably occurred (Sale 1979; Connell 1983). Persson's (1986) experiment of the opposite situation, that of removing a competitor, showed competitive release through increased food consumption, sizes of prey eaten, and individual growth rates in perch (*Perca fluviatilis*).

To test our hypothesis that white perch compete with yellow perch for a food-limited resource in Lake Erie, we determined consumption rates, examined diet overlap and growth of white perch, and compared these data with those for yellow perch. Knowledge of not only the prey type, but also of the amount

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of prey eaten is important in determining the degree of interaction and resource partitioning. Based on these interactions, reduced growth in Lake Erie yellow perch would implicate white perch as a competitor.

Materials and Methods

Fish Collection

Collections of white and yellow perch were made in 1983 through 1985 from bottom trawls fished in alternate weeks from May to November at 10 stations in the central and western basins of Lake Erie (Fig. 1). Samples of white perch and yellow perch from diel trawling (two 10-min bottom tows every 3 h for 24 h) were collected in 1983 and 1984. Diel samples were taken from one western basin site (near Middle Sister Island) and one central basin site (off Fairport, Ohio) three times during the collecting season, usually in May, July, and September. In 1987, diel trawling was done in May and July at a site in the western basin (near Green Island).

All white perch and yellow perch in 1983–85 were frozen in the field on dry ice to deter digestion or regurgitation of stomach contents. In 1987, fish were placed on ice and then transferred to a freezer within 1 h after collection. White perch were sexed, weighed to the nearest gram, and measured to the nearest millimeter total length (TL) and scale samples were taken for aging. Stomach and intestinal contents were weighed (wet and dry after 24 h at 80°C). Fish showing evidence of regurgitation were not used to determine food consumption. All yellow perch data from 1983–85 were obtained from Hayward (1988).

Daily Food Consumption

Amounts of food (g) in individual stomachs from each trawl haul were determined to estimate quantities of food consumed over 24-h. The amount of food in a stomach was expressed as the ratio of total weight of food material to total weight of the fish (weight–specific food quantity). Medians (and quartiles) of weight–specific food quantities ($g \cdot g^{-1}$) were determined from each of the successive trawl collections. We converted point estimates (at 3-h intervals) of median food amounts in stomachs ($g \cdot g^{-1}$) to daily consumption rates ($g \cdot g^{-1} \cdot d^{-1}$) by using the exponential algorithm of Elliott and Persson (1978). Instantaneous rates of gastric evacuation (R) for white perch were estimated from a relation developed by using experimental and diel field data (Parrish and Margraf 1990).

We also estimated daily food consumption ($g \cdot g^{-1} \cdot d^{-1}$) for white perch from single trawl hauls made from 0800 to 2000 hours, following the correlative method used by Hayward and Margraf (1987). In this method, median weight–specific food quantities from these peak feeding hours were multiplied by our white perch temperature-dependent gastric evacuation rate (R) and then regressed against calculated diel consumption rates. From the collections made from 0800 to 2000 hours, we derived five regression relationships (Fig. 2). Our r^2 values compared well with those obtained by Hayward and Margraf (1987) for yellow perch at 1100, 1400, and 1700 hours ($r^2 = 0.87$, 0.84, 0.91). Single trawl ($g \cdot g^{-1}$) values of the weight–specific food quantities were then converted to daily consumption ($g \cdot g^{-1} \cdot d^{-1}$) by using the regression from the time nearest to the actual trawling time. Like yellow perch, white perch were sometimes absent from the summer diel samples; therefore the correlative method was used to estimate food consumption for the 24-h period.

White perch consumption rates were compared between basins to determine if white perch and yellow perch were being subjected to similar interbasin differences in feeding conditions (Hayward and Margraf 1987). Consumption rates were compared between species within each basin.

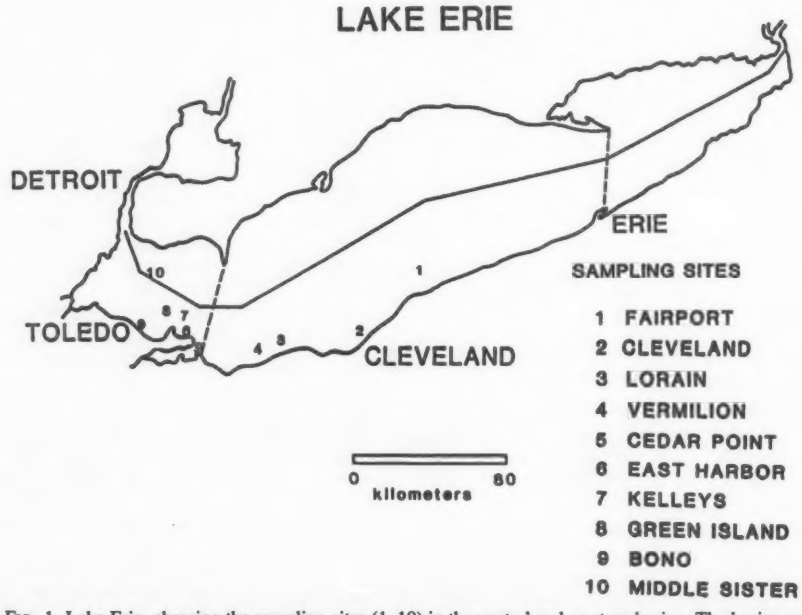

FIG. 1. Lake Erie, showing the sampling sites (1–10) in the central and western basins. The basins are divided by the vertical dashed lines. United States and Canadian waters are divided by the longitudinal line.

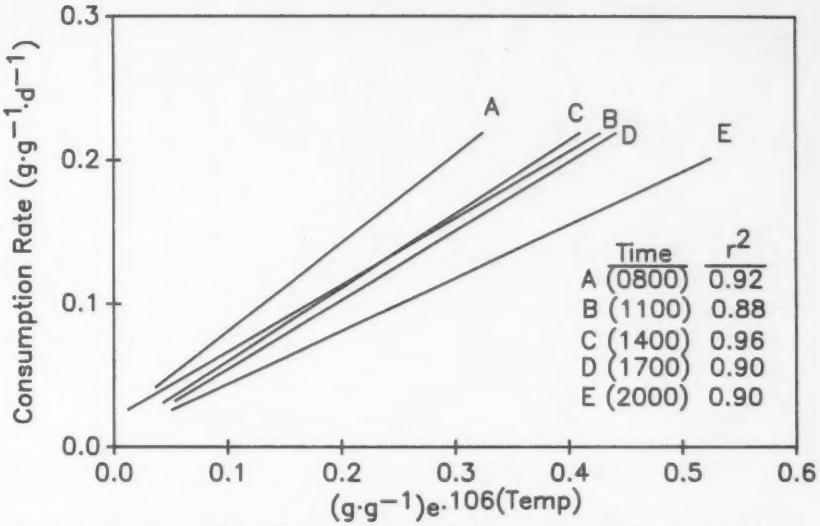

FIG. 2. Least-square regressions of time-specific white perch temperature-adjusted median weight-specific food ratios and calculated 24-h diel consumption rates from 1983 and 1984.

TABLE 1. Prey eaten by white perch (WP) and yellow perch (YP) in Lake Erie from 1983 (Year 1), 1984 (Year 2), and 1985 (Year 3). Numbers are mean percent biomass from all sampling dates and sites.

	Spring						Summer						Fall					
	WP			YP			WP			YP			WP			YP		
	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Zooplankton																		
Cladocera																		
Bosmina															1			
Chydoridae	4	<1	—	<1	—	—	1	—	3	—	<1	3	<1	16	63	<1	14	32
Daphnia	13	47	49	7	33	17	45	87	62	13	58	24	42	29	—	1	26	4
Eubosmina	2	<1	—	<1	<1	—	1	—	—	—	<1	—	—	4	—	—	<1	—
Leptodora	7	6	<1	6	2	—	33	3	<1	43	6	3	2	6	1	36	6	11
Sidadae	—	—	—	—	—	—	—	—	—	—	<1	—	<1	<1	—	—	—	<1
Copepoda																		
Calanoida	—	4	—	—	2	—	—	—	4	—	—	—	—	—	—	—	—	—
Cyclopoida	3	5	9	<1	4	7	—	—	4	—	—	1	4	5	7	2	8	2
Macroinvertebrate																		
Amphipoda	—	—	—	—	<1	1	—	—	<1	—	—	<1	1	3	—	—	<1	—
Chironomidae	68	27	41	83	51	74	20	2	20	26	10	57	39	21	18	46	23	31
Hirudinea	—	<1	—	<1	1	—	—	—	—	—	—	—	—	<1	—	1	—	1
Hydracarina	—	1	<1	—	—	—	—	—	—	—	<1	—	—	3	5	—	1	<1
Isopoda	2	7	—	—	3	—	—	—	—	—	—	—	8	1	—	—	—	—
Nematoda	—	<1	—	—	<1	—	—	—	—	—	—	—	1	<1	5	—	—	-
Oligochaeta	—	<1	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—
Ostracoda	1	1	—	—	2	1	—	—	—	—	—	—	—	1	<1	—	<1	—
Sphaeriidae	—	—	—	3	1	—	—	—	—	14	—	—	2	—	<1	4	2	4
Fish[a]	—	1	—	<1	<1	1	—	8	6	2	25	8	—	10	—	10	18	14

[a]Primarily gizzard shad, rainbow smelt, white perch, white bass, and yellow perch.

Diet Composition and Overlap

Stomach contents of white perch and yellow perch were identified to the same taxonomic level (Table 1). Percent diet composition was determined by using accepted length–weight regressions of the available prey, which included zooplankton, benthic organisms, and fishes (P. K. Cunningham, Minnesota Department of Natural Resources, MN and G. G. Mittelbach, Michigan State University, Kellogg Biological Station, MI, pers. comm.). Diet overlap for fish caught at the same time, on the basis of size of food and taxonomic composition, were determined by using the Schoener (1970) index, the most commonly used diet overlap index (Wallace 1981). Because few

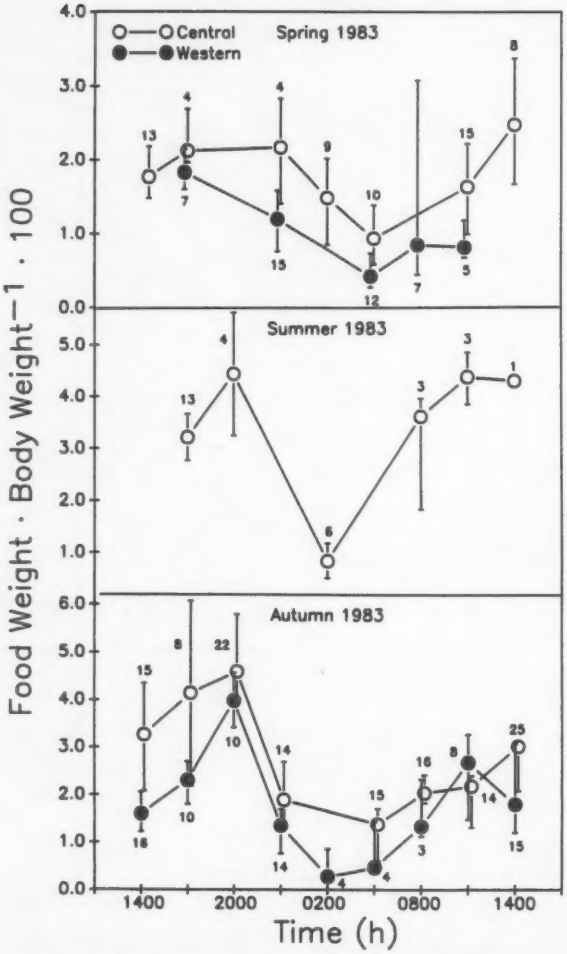

FIG. 3. Medians and quartiles of weight-specific food percentages (food weight·body weight^{-1}·100) for diel-sampled white perch (85–205 mm long) from the central and western basins of Lake Erie in 1983.

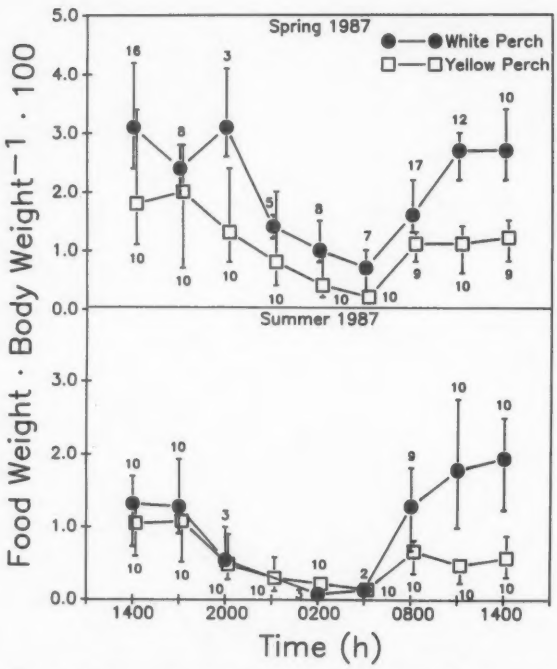

FIG. 4. Medians and quartiles of weight-specific food percentages (food weight·body weight^{-1}·100) for diel-sampled white perch and yellow perch (85–205 mm long) from the western basin of Lake Erie in spring and summer 1987.

fish were eaten by either species, we lumped all fish species into a single category for use in the Schoener index.

Growth Measurements

White perch in excess of 15 individuals from trawl collections were reserved for growth determination. These fish were sexed, measured, and aged from scale samples, and wet weights and dry weights of whole specimens were determined. Dry weights were obtained after specimens were dried for 72 h at 80°C and used to derive a regression of dry weight against wet weight. Sizes-at-age of white perch were compared between basins and then between white perch and yellow perch within each basin.

Results

Daily Food Consumption

White perch collected in the central basin during diel sampling in 1983 generally had more food in their stomachs than fish from the western basin (Fig. 3). Food amounts (g·g^{-1}·100) in the stomachs from the central basin were greater in three of the four comparison times in spring (Wilcoxon Rank Sum, $P>0.1$), with the greatest difference of 50% occurring at 2300 hours. In the fall diel samples, food amounts in central basin fish were significantly higher in six of eight time periods. In spring 1987 in the western basin, median amounts of food in white perch stomachs were approximately 16–58% greater than in yellow perch stomachs at all times during the 24-h period (Fig. 4). However, food amounts at only four of the nine times differed significantly (Wilcoxon Sign Rank, $P>0.1$). Because the rate of food evacuation increased at high summer temperatures, the data were similar except during times of high feeding (0800–1400 hours), when food amounts in white perch were statistically greater than those in yellow perch.

The average daily consumption rates of white perch in diel samples taken in 1983–84 and 1987 ranged from 0.026 to 0.219 g·g^{-1}·d^{-1} (Table 2). Generally, consumption rates of white perch, like those of yellow perch, were higher in the central than in the western basin. In addition, white perch ate more food than yellow perch in 10 of the 12 diel samples (Fig. 5). We also calculated consumption rate differences between species from single semimonthly trawl values (1983–85) using the correlative method (Fig. 6). Food consumption by white perch exceeded that of yellow perch throughout the sampling season. The greatest differences, as much as 27%, were in July.

Diet Composition and Overlap

According to our lakewide combined data, white perch fed on a wide variety of organisms (Table 1). As an example of

TABLE 2. Consumption rates of white perch (85–205 mm long) for 1983–84 diel samples from the western and central basins and in 1987 from the western basin of Lake Erie. In two western basin diel samples, white perch were not caught at enough of the time periods to calculate consumption rates.

	Food consumption ($g \cdot g^{-1} \cdot d^{-1}$)	
Season	Western basin	Central basin
1983		
Spring	0.032	0.052
Summer	—	0.219
Fall	0.137	0.198
1984		
Spring	0.026	0.026
Summer	0.097	0.121[a]
Fall	—	0.052[a]
1987		
Spring	0.068	
Summer	0.074	

[a]Consumption rate calculated from regression.

prey consumed at a single site, Fairport in fall 1983, organisms of 18 taxa were consumed, although only seven of the taxa contributed 1% or more of the total weight of food (Parrish 1988). Increased diet breadth was apparent when white perch were eating more benthos rather than zooplankton. They fed more heavily on benthic organisms such as chironomids in spring, but switched to more zooplankton in summer. In fall, both benthos and zooplankton were eaten.

White perch and yellow perch in Lake Erie ate a major proportion of the same prey items (Table 1). The diet overlaps were significant (Schoener Index >0.6) in 25 of the 48 comparisons (52%). Less than significant overlap comparisons were most frequent when yellow perch ate more benthos than did white perch. Low Schoener values were also attributed to a greater frequency of piscivory by yellow perch. Diet overlap values throughout the sampling season differed among sampling years (Fig. 7), with the frequency of significant diet overlaps greatest in 1983 and smallest in 1985. On a seasonal basis, overlap values were generally lowest in spring and fall, however, some of the highest values were also recorded in spring.

We examined the possibility that the range in white perch and yellow perch total lengths (85–205 mm) used in the diet overlap calculations were responsible for the low overlap values (<0.6); e.g. diets of small white perch compared to those of large yellow perch. Diet overlaps using the narrower size ranges (85–139 mm and 140–205 mm long) were determined where sample size permitted and the resulting overlap values were not greater than those previously determined for the broader size range.

Growth

To evaluate white perch growth, we examined differences in size at age of white perch throughout a single season (1983). There were no large interbasin differences in wet weights of 1- and 2-y-old white perch, from the four central basin sites and one western basin site (Fig. 8a). The data for yellow perch, in contrast to the data for white perch, showed large interbasin differences in weight at ages 2 and 3 (Fig. 8b). Too few white perch of age 3 were collected in 1983 for comparisons.

Discussion

White perch from the central basin ate more food than those from the western basin. This is similar to the pattern shown by larger yellow perch (140–205 mm long) and to a lesser degree by small yellow perch (85–139 mm long) in 1983 (Hayward and Margraf 1987). The 1984 data for small yellow perch also showed large interbasin differences in consumption in the summer and fall diel samples (Hayward 1988).

Consumption rates of white perch were as much as 27% greater than those of yellow perch. In 1983, consumption ranged from 1.7 to 9.6% body weight in 85–135 mm yellow

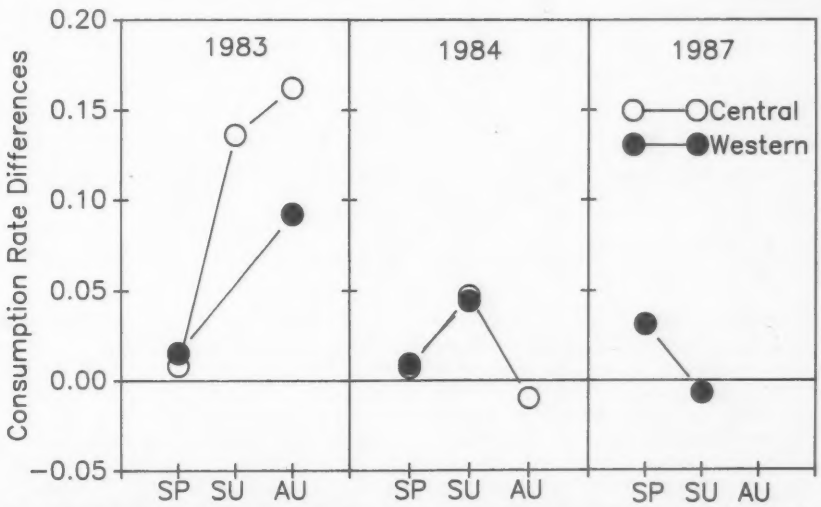

FIG. 5. Differences in white perch and yellow perch average daily consumption rates ($g \cdot g^{-1} \cdot d^{-1}$) calculated from spring (SP), summer (SU), and fall (AU) diel sampling in the central and western basins of Lake Erie in 1983–84 and in the western basin in 1987. Positive values favor white perch.

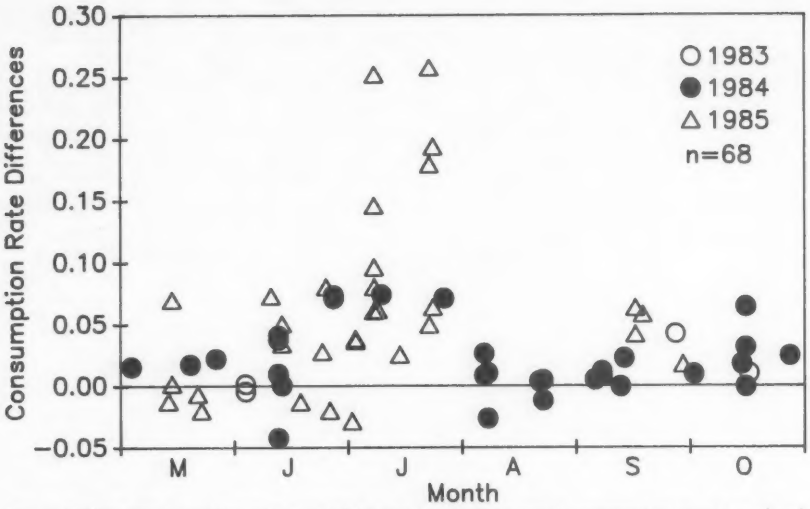

FIG. 6. Differences in median values of white perch and yellow perch consumption rates ($g \cdot g^{-1} \cdot d^{-1}$) calculated with single-trawl data by using the correlate method. The trawl data were collected throughout the 1983–85 sampling seasons and each data point represents a minimum of three fish of each species. Positive values favor white perch.

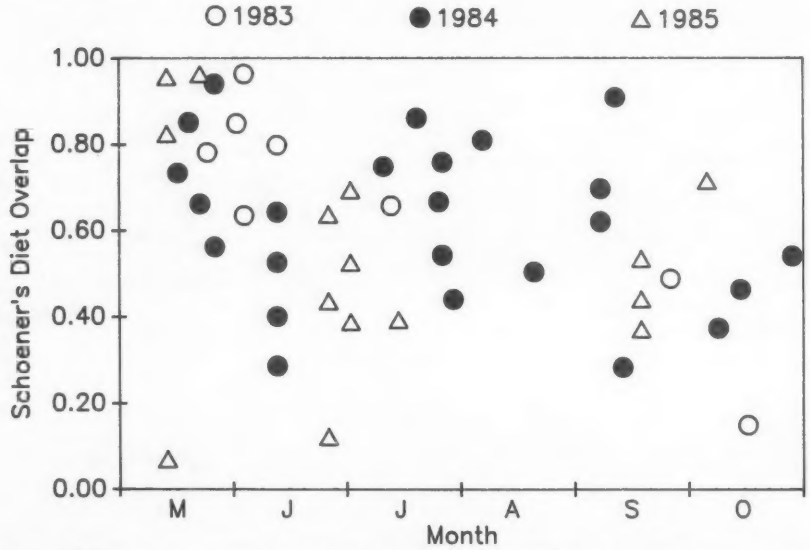

FIG. 7. Schoener's diet overlap index values from collections throughout the sampling seasons (May–October 1983–85).

perch (Hayward and Margraf 1987), and from 3.2 to 21.9% in 85–205 mm white perch. Maximum food consumption rates are greater for smaller fish of a species. Most of the white perch fell into the lower end of the size range. The inclusion of larger fish in the calculations would presumably decrease the median consumption rate of white perch. Comparing these rates to those of the small yellow perch would therefore result in the most conservative estimate of consumption rate differences between the two species.

The daily rations we determined for white perch are some of the highest reported for any of the fishes. We could find no other studies that determined rations for white perch in other waters. However, for yellow perch (83–150 mm long), Nakashima and Leggett (1978) estimated daily ration in Lake Memphremagog, Quebec — Vermont to range from 2.2% in October to 6.7% in July. These results are comparable to those yellow perch in Lake Erie.

In general, white perch are opportunistic feeders with broad, plastic diets (Zuerlein 1981; Stanley and Danie 1983). Although white perch in Lake Erie ate mostly invertebrates, as they do in other waters, their diets differed from those reported in other studies. Bath and O'Connor (1985) concluded that white perch in the Hudson River ate primarily benthic epifauna and infauna; they found mostly crustaceans, insect larvae, and annelid

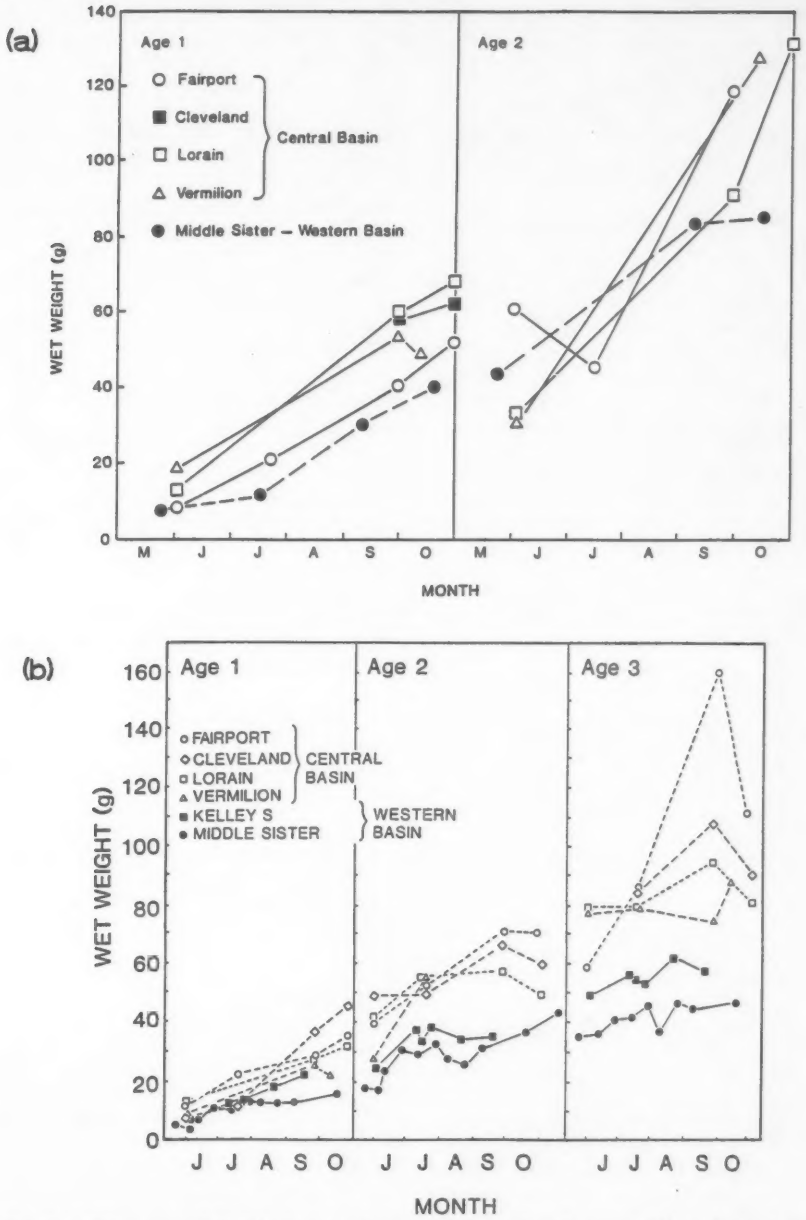

FIG. 8. (a) Mean wet weights (g) of age 1 and age 2 white perch from four central basin sites and one western basin site throughout the sampling season in 1983. (b) Mean wet weights (g) of yellow perch of ages 1, 2, and 3 from four central basin sites and two western basin sites throughout the sampling season in 1983 (Hayward and Margraf 1987).

worms. Generally, white perch ate benthos almost exclusively over zooplankton (Zuerlein 1981; Minns and Hurley 1986). On the other hand, Elrod et al. (1981) found that age 2 white perch were mainly piscivorous in Lake Ontario.

In Lake Erie, although white perch ate significant amounts of benthic organisms, fish of all lengths (85–205 mm long) ate zooplankton if it was abundant. When the larger zooplankters were not available, white perch ate smaller organisms such as copepods and *Eubosmina*. They appeared to be able to adapt to available prey and yet maintain high consumption rates. Our results differ from the previous information on Lake Erie white perch diets published by Schaeffer and Margraf (1986a); in September 1981, 77% of the white perch diet consisted of gizzard shad.

Diet overlap values were most variable in spring, ranging from the lowest to the highest. In spring and occasionally in the summer when chironomids were emerging, yellow perch ate chironomids almost exclusively; white perch also preyed heavily upon chironomids, but when a divergence occurred, white perch usually fed more on zooplankton. This divergence in diet, when yellow perch ate benthos while white perch were feeding on zooplankton, was especially apparent in the fall samples (Parrish 1988). In some of the summer and fall samples, fish were eaten by yellow perch more than by white perch. In all of the diet overlap values calculated and where the index was not significant ($n=48$), white perch ate more fish than yellow perch in only one instance.

Diet overlap values are more relevant when examined in relation to food consumption rates. A paradoxical situation occurs when white perch feed on zooplankton and yet maintain high consumption rates. At the same time, yellow perch are feeding on the larger bodied benthos or fish, but their consumption rates are often at or below maintenance level (Hayward and Margraf 1987). A possible explanation is that white perch are simply efficient zooplanktivores, even as adults. They are less subjected to the ontogenetic shifts in diet that are imperative to yellow perch (Schneider 1972; Hayward and Margraf 1987). Although the white perch is similar morphologically, it has a more nearly terminal mouth, which is advantageous in feeding up in the water column. The somewhat more subterminal mouth of yellow perch makes it easier for them to feed at the bottom.

In Lake Ontario, Elrod et al. (1981) and Hurley (1986) found that white perch and yellow perch ate similar prey. They concluded that the high overlap in diets was caused by the similar availability of organisms. Chironomids and macrocrustaceans, which were among the most abundant benthic organisms, were consumed heavily by both species. Because of the sparsity of benthic organisms in Lake Erie (Hayward and Margraf 1987), some partitioning of that limited resource appears to occur, except when benthic organisms are abundant (e.g. during chironomid emergence).

Based on size at age data, we could not detect distinct interbasin growth differences of adult white perch. Even if white perch are growing faster in the central basin than in the western basin, the small difference was not comparable to that shown by yellow perch.

Hayward and Margraf (1987) clearly attributed interbasin yellow perch growth difference to reduced food consumption by fish in the more eutrophic western basin. Although white perch show similar differences in patterns of food consumption, they did not show a similar growth pattern. Possible explanations for this difference lie in physiological requirements of the two species. The thermal optimum for yellow perch is reported to be 23°C (Schneider 1973; the maximum observed preference of 29°C in the laboratory and 27°C in the field (Hokanson 1977)). The optimum for white perch is at least a few degrees higher; several thermal optima have been reported ranging from 5°C to 32°C, which depend on the acclimation temperature (Stanley and Danie 1983). Kellogg and Gift (1983) determined that the optimum growth temperature for young white perch (about 30 mm long) was 28.5°C.

Differences in thermal preferenda between the two species may alter their separate abilities to use the food available. Although differences in thermal regimes in the central and western basins of the lake are not responsible for the large interbasin growth differences of yellow perch (Hayward and Margraf 1987), their effects on white perch may be greater. Higher thermal preference and thus reduced energetic costs may enable white perch to eat less in the western basin and still maintain growth similar to that in the central basin.

Interbasin mixing of populations offers another plausible explanation for our failure to observe growth differences of white perch in the two basins. Movements of white perch are not generally understood. Although they are not noted for swimming long distances within their natural range in east coast estuaries, the populations of the central and western basins of Lake Erie may congregate at various times. Most likely this would occur in the rivers of the western basin during spring spawning, as occurs with white perch moving to the shallow areas of the Bay of Quinte during spawning (Minns and Hurley 1986). Such non-discrete interbasin populations in Lake Erie would make differences in growth difficult to detect.

Although direct evidence for competition can be determined only through experimentation (Hanson and Leggett 1986), we have shown that the potential for competition between white perch and yellow perch in Lake Erie is high. Although we agree with Hayward and Margraf (1987) that the eutrophication of Lake Erie is a mechanism that is responsible for the beginnings of the disparate interbasin growth in yellow perch, this disparity has increased since the arrival of white perch. Hanson and Leggett (1982) found that fish biomass was strongly correlated to available macrobenthos biomass. Given the existence of limited food (Hayward and Margraf 1987), especially in the western basin of Lake Erie, we conclude that yellow perch have been negatively affected by the invasion of white perch.

Acknowledgments

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Ratios in Aquatic Sciences: Statistical Shortcomings with Mean Depth and the Morphoedaphic Index

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Researchers in aquatic sciences frequently employ empirically derived models to predict productivity, yield, and abundance of fish. We demonstrate that predictive models employing ratios of standardized biomass and lake morphometric variables are biased by spurious correlations due to mathematical transformations and the use of inappropriate null models. Our findings emphasise that studies incorporating ratios like mean depth or the morphoedaphic index require cautious interpretation. Future research should focus on more appropriate analytical approaches such as regression-based models like the analysis of covariance. Alternatively, where ratios are employed and spurious correlations are likely, statistical evaluations must incorporate randomization tests to assess the significance of such results.

Les chercheurs en sciences halieutiques utilisent fréquemment des modèles empiriques pour prévoir la productivité, le rendement et l'abondance du poisson. Nous démontrons que les modèles prédictifs fondés sur des rapports de variables normalisées relatives à la biomasse et à la morphométrie des lacs sont faussés par des corrélations illégitimes attribuables aux transformations mathématiques et à l'utilisation de modèles nuls inappropriés. Nos travaux montrent que les études faisant intervenir des rapports comme la profondeur moyenne et l'indice morphoédaphique nécessitent une interprétation très prudente. Dans l'avenir, la recherche devrait être orientée vers des approches analytiques plus appropriées, comme les modèles fondés sur la régression, par exemple, l'analyse de covariance. On peut aussi, là où l'on utilise des rapports et où les corrélations illégitimes sont vraisemblables, incorporer des tests de randomisation dans les évaluations statistiques pour évaluer la signification de ces résultats.

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Scientists often construct predictive models of biological, physical, and chemical processes. Many models in aquatic and fisheries sciences resulted from intensive studies conducted during the 1930's, 40's and 50's (e.g. Rawson 1930, 1952; Rounsefell 1946; Northcote and Larkin 1956; Hayes 1957). Such studies sought management tools to predict potential harvest or yield according to combinations of physical and chemical limnological variables. At that time the complex calculations required to analyze data often prompted reductions in the number of variables, frequently through the use of compound or ratio variables. Ratios facilitated interpretation and even straightened curvilinear relationships between variables. For example, Rawson (1952) found that fish and invertebrate densities exhibited a hyperbolic relationship with lake mean depth (mean depth is the ratio of volume to area representing the average lake depth; see Rawson 1952, 1955). Subsequently, Ryder (1965) straightened this relationship by using the reciprocal of mean depth. Additional predictive power was obtained by incorporating a measure of productivity (i.e. total dissolved solids per unit volume, TDS) to produce a compound variable termed the morphoedaphic index (MEI; e.g. Ryder 1965, 1982; Ryder et al. 1974). The apparent increased predictive ability of ratios provided complex models incorporating many variables in regression and correlation analyses. Such use of ratios is common in biological sciences (Packard and Boardman 1988), and aquatic sciences in particular (Kenney 1982). The implications of using ratios in statistical analyses were recognized first by Pearson (1897) and more recently by Chayes (1971), Atchley et al. (1976), Kenney (1982), Gibson (1984), and Packard and Boardman (1987, 1988). Nonetheless, many scientists appear unaware of the difficulties created by the use of ratios, or simply choose to ignore the problems (Jackson and Somers 1990).

Ratios and compound variables have many statistical properties that compromise their use (e.g. Atchley et al. 1976; Kenney 1982; Pendleton et al. 1983; Phillips 1983; Gibson 1984; Green 1986). Among these are: (1) lack of normality (Atchley et al. 1976); (2) the assumption that the numerator and denominator are collinear with an intercept of zero (Packard and Boardman 1987, 1988); and (3) spurious correlations (Chayes 1971; Atchley and Anderson 1978; Kenney 1982; Pendleton et al. 1983). Our study is restricted to the effects of spurious self-correlations from using ratios in the aquatic sciences, specifically the use of mean depth and the MEI to predict biomass, yield, or production.

Because computers are now widely available, the justification for using ratios or products (i.e. multiplying two or more variables to form a compound variable) to reduce complex calculations is gone, but the practice persists, perhaps because ratios are both conceptually appealing and traditional (Phillips 1983). The availability of nonlinear regression and correlation techniques, plus methods incorporating multiple variables (e.g. multiple regression, principal components analysis, analysis of covariance) reduces the need to use ratio variables. However,

traditional ratios such as mean depth and the MEI remain, and new ratios continue to be proposed (e.g. biomass per unit area divided by mean depth, Hanson and Leggett 1982; mean depth divided by maximum depth; Wetzel 1983 pages 33–35).

Typically, studies examining the properties of ratios are criticized for using simulated rather than real data (e.g. Dodson 1978). Such criticisms appear to be based on the perception that analyses and results differ between simulated and sampled data. To avoid a similar criticism and to illustrate the problems associated with ratios, we use correlation analyses of both simulated and published data. We focus our study on simple predictive bivariate models of fish yield (or abundance) relative to lake morphometry (i.e. mean depth and MEI) because these models have an extensive history and widespread continuing use in aquatic sciences.

Lake mean depth has been described as the most significant morphometric variable in comparing lakes (Ryder et al. 1974) because it is highly correlated with other measures such as lake thermal conditions, productivity, and euphotic-zone depth. Thus, mean depth provides a surrogate measure of many variables that require long-term intensive sampling (e.g. thermal budgets). We also employ the inverse of mean depth, as this ratio is often used to straighten the relationship between biomass and mean depth (see above). In addition, the inverse of mean depth is a component of the MEI (Ryder 1965) and over 100 studies have used the MEI (Ryder 1982; Hanson and Leggett 1982). Although we have focused on the use of mean depth and the MEI, our results have general applicability whenever ratios or products are incorporated into predictive models. We provide examples to show that studies using ratios in empirical models often incorrectly assess and interpret results because inappropriate null models and statistical tests are used.

Methods

Simulated Data

We generated three normally distributed variables, each with a mean of 100 and standard deviation of 30. The three variables were generated independently of one another (i.e. correlations of 0) and were named lake surface area, fish biomass per lake, and lake volume (*A*, *B*, and *V*) to parallel the published data examples cited below. Using these variables, we derived several ratios of a form commonly used in the aquatic sciences. We calculated correlations for each of the following relationships:

- *B* vs. *A* (total biomass vs. lake area);
- *B*/*A* vs. *A* (biomass per unit area vs. lake area);
- *B*/*A* vs. *V*/*A* (biomass per unit area vs. lake mean depth);
- *B*/*A* vs. *A*/*V* (biomass per unit area vs. the inverse of mean depth); and
- log(*B*/*A*) vs. log(*V*/*A*) (log biomass per unit area vs. log of mean depth).

We used both Pearson product–moment correlations and Spearman rank correlations to assess the strength of the association between variables. To determine the probability of rejecting the null hypothesis for each of these correlations, we used randomization tests. Although our simulated data met the statistical assumptions necessary for correlation analysis (e.g. normal distribution, random sampling), biological data typically do not. Edgington (1987) stresses that statistical tables only approximate the correct probabilities provided by randomization tests when such assumptions are not met. Because the second part of our study examines published data sets that fail to meet these assumptions, we use randomization tests throughout to evaluate the significance of the Pearson and Spearman correlation coefficients.

The probability estimate obtained from a randomization test is calculated as follows (e.g. see Edgington 1987). A correlation between *B* and *A* is calculated to obtain the observed correlation (i.e. r_{obs}). One of the variables (i.e. *B*) is randomly permuted under the assumption that there is no inherent association between *B* and *A* (i.e. fish biomass per lake is independent of lake area). The correlation for *A* and the randomised data for *B* is calculated, *B* permuted again and the correlation recalculated. This form of permutation and calculation of the correlation coefficient is done 999 times to derive a probability density function for the coefficient (i.e. the expected 'random' distribution). Since we are interested in whether r_{obs} is greater than expected by chance, we count the number of randomized correlations with an equal or more extreme value. If we expect a positive correlation between *B* and *A*, we count the number of random correlations with an equal or greater positive value than r_{obs} (i.e. a one-tailed test). If we find 29 random cases with coefficients equal to or exceeding the r_{obs}, the probability of finding as extreme a correlation is $\frac{30}{1000}$ or 0.030 (i.e. 29 random cases plus 1 observed case divided by a total of 1000 correlations).

Published Data

Ten data sets comprising lake surface area (*A*), mean depth ($\bar{z}$ or lake volume divided by area; *V*/*A*), and fish yield (or abundance) were selected from the literature (see Table 1). Most data sets presented yield in a standardised form (i.e. *B*/*A*; $kg \cdot ha^{-1} \cdot yr^{-1}$) although the data were collected as the total yield per lake (*B*; e.g. Rawson 1952). Therefore, we calculated total lake yield (i.e. $kg \cdot yr^{-1}$) as the product of lake area and fish yield per unit area. Because lake mean depth is defined as lake volume divided by lake area, lake volume was calculated as the product of lake area and mean depth.

To evaluate the effects of using ratio variables, we generated a number of ratios that are commonly used in aquatic sciences. The first was *B*/*A* (biomass per unit area) because total catch or production for a given lake is typically standardized per unit area to remove the influence of lake size. The ratio of the inverse of lake mean depth $\left(\text{i.e. } \frac{1}{\bar{z}} \text{ or } A/V\right)$ as incorporated into the MEI $\left(\text{i.e. } \frac{\text{TDS}}{\bar{z}}\right)$ was evaluated. We chose not to include TDS in our analysis as Ryder (1982, page 156) stated that a "generalized morphoedaphic expression ... would have mean depth in the denominator and any one of a number of ions in the numerator." Therefore, the form $\frac{1}{\bar{z}}$ or *A*/*V* represents the most generalized form of the MEI although it does not include an edaphic component per se.

We examined the same relationships as with the simulated data to determine the effects of spurious self-correlations on the null or expected distribution of Pearson and Spearman coefficients. The implicit assumption in studies examining the 'bivariate' relationship between yield and lake area, mean depth, or the MEI is that the expected correlation coefficient from a ran-

TABLE 1a. Pearson and Spearman rank correlations for published data sets. Significance levels determined by randomization tests. r_o = observed correlation coefficient; r_m = median correlation coefficient from randomization test; all correlations are multiplied by 1000.

	Rawson 1952 ($N=13$)			Rawson 1961 ($N=12$)			Hayes 1957 ($N=56$)			Ryder 'A' 1965 ($N=23$)			Ryder 'B' 1965 ($N=11$)		
Variables	r_o	r_m	P	r_o	r_m	P	r_o	r_m	P	r_o	r_m	P	r_o	r_m	P
B·A	523	052	044	739	−077	033	963	051	001	664	−073	004	986	−111	001
B/A·A	−561	−455	145	−577	−438	044	−069	−066	404	−430	−178	001	−494	−179	001
B/A·V/A	−760	−392	001	−563	−425	171	−366	−043	001	−613	−205	001	−583	−175	001
B/A·A/V	681	580	387	461	319	305	577	−007	001	565	599	555	627	−069	122
Log(*B/A·V/A*)	−895	−560	006	−662	−659	482	−368	−161	008	−827	−612	005	−774	−461	026
Rank(*B·A*)	824	−011	001	804	210	001	692	003	001	967	−021	001	927	018	001
Rank(*B/A·A*)	−582	−780	985	−795	−867	844	−445	−002	387	−632	−752	909	−118	−618	991
Rank(*B/A·V/A*)	−769	−670	168	−655	−706	322	−297	−142	052	−756	−609	065	−627	−164	018

TABLE 1b.

	Matuszek 1978 ($N=22$)			Hanson and Leggett #1 1982 ($N=26$)			Hanson and Leggett #2 1982 ($N=21$)			Hanson and Leggett # 3 1982 ($N=20$)			Bayley 1988 ($N=24$)		
Variables	r_o	r_m	P	r_o	r_m	P	r_o	r_m	P	r_o	r_m	P	r_o	r_m	P
B·A	632	−068	023	668	−050	007	728	−056	002	995	−086	001	863	−044	001
B/A·A	−308	−247	158	−082	−135	1000	−006	−228	1000	102	−089	1000	282	−217	110
B/A·V/A	−432	−262	008	−026	−183	061	372	−139	1000	−232	−133	005	−245	−157	028
B/A·A/V	505	228	099	028	508	996	−354	274	1000	590	236	006	653	030	029
Log(*B/A*)·log(*V/A*)	−549	−650	853	−157	−597	1000	429	351	665	−532	−462	328	−419	−411	468
Rank(*B·A*)	892	−014	001	964	001	001	932	016	001	950	−006	001	673	−001	001
Rank(*B/A·A*)	−550	−773	997	−166	−677	1000	569	−546	1000	−191	−705	1000	−344	−644	995
Rank(*B/A·V/A*)	−486	−661	952	−196	−620	1000	458	−352	1000	−552	−477	290	−322	−373	631

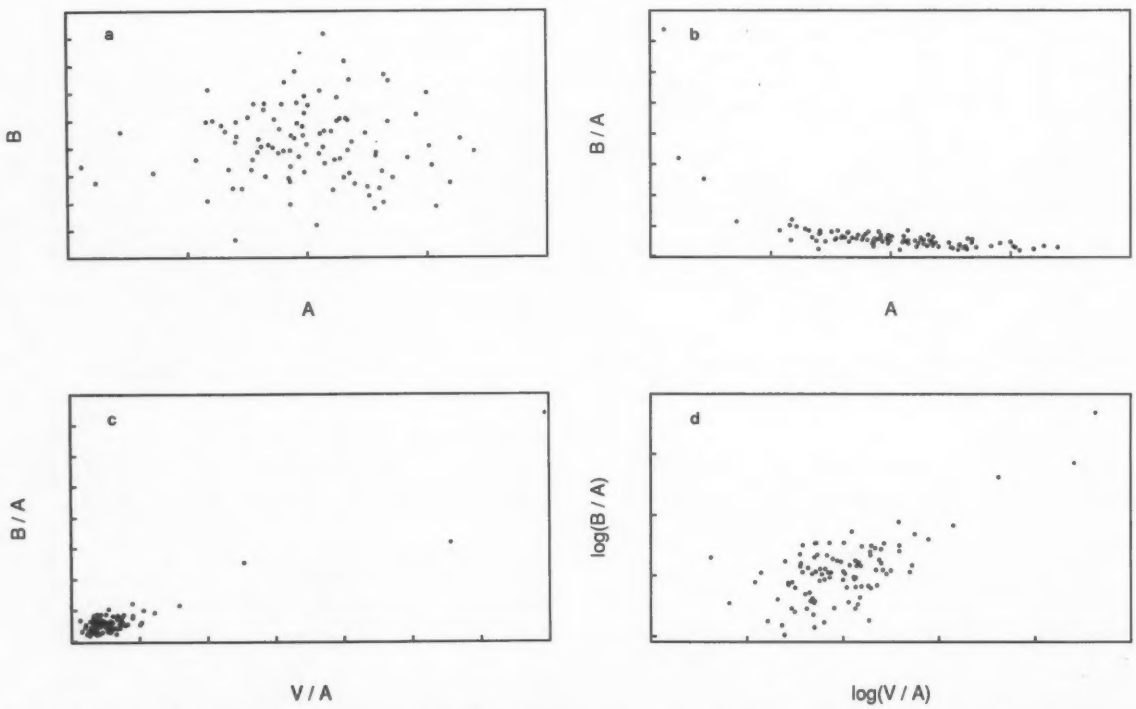

FIG. 1. Scatterplots of simulated data ($N=100$) showing spurious relationships due to ratio formation. Variables, *A*, *B*, and *V* are independently generated data from a normal distribution with a mean of 100 and standard deviation of 30.

dom data set is zero (i.e. the null hypothesis is that the correlation coefficient $r = 0$). If this assumption is not met (as well as others identified above), then standard tables for probabilities of correlation coefficients are not adequate. To resolve this problem and the lack of random sampling, we evaluate correlation coefficients with randomization tests. We exclude

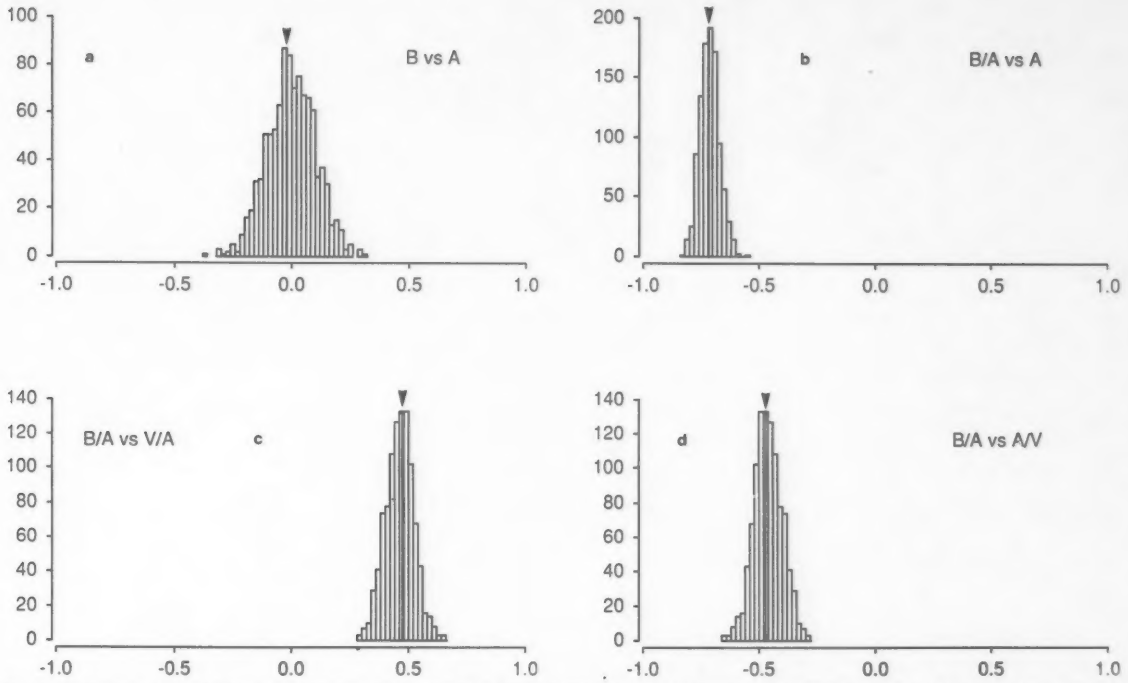

FIG. 2. Frequency distributions of Spearman rank correlation coefficients from 1 000 permuted correlations of the simulated data. Observed correlations from Fig. 1 are indicated by arrows. Note that the distribution shifts from 0 when ratio variables are analyzed.

recently proposed ratios (e.g. benthic biomass per unit area divided by mean depth; Hanson and Leggett 1982), because the following examples are sufficient to illustrate our point.

Results

Simulated Data

The effect of ratio generation is readily apparent (Fig. 1). An initially random configuration of points (Fig. 1a) is transformed into the classical nonlinear curve (Fig. 1b) described by numerous authors (e.g. Rawson 1952, 1961; Ryder 1965, 1982; Ryder et al. 1974). The rank correlation has changed from -0.022 for B with A to -0.716 for B/A with A which is different from 0 ($P < 0.001$) using traditional statistical tables. The subsequent division of the numerators B and V by A produces a positive relationship (Fig. 1c) that provides a rank correlation of 0.471 whereas the Pearson correlation has increased to 0.926. Again, both of these correlations differ from $r = 0$ ($P < 0.001$) using tabulated values).

The randomization test permits an evaluation of the observed correlation relative to the expected values assuming a random bivariate association. The rank correlation coefficients from the randomization test of B and A are centred on 0 and show a distribution similar to a normal curve as expected (Fig. 2a). The simple 'standardization' of biomass in the form of dividing by area (i.e. B/A) shifts the centre of the distribution from 0 to -0.701 and the variance around this value has been reduced greatly (Fig. 2b). We also note that the traditional tabulated null correlation of 0 no longer falls within the boundaries of the randomized values because of a spurious correlation as A now appears in both variables. The distribution of coefficients for B/A and V/A (i.e. biomass per unit area and lake mean depth) is centred on 0.49 and, again, 0 does not fall within the distribution (Fig. 2c). Identical results are found for the rank correlation of B/A with the inverse of mean depth (i.e. A/V; Fig. 2d) although the distribution is centred about a value of -0.49. Note that the observed correlations for the simulated data (indicated by arrows) are found in the centre of each distribution. These values are expected because the variables A, B and V were independently generated and therefore have no inherent inter-relationships (i.e. they are random variables; but note the strong spurious correlations).

Distributions for the Pearson correlation coefficients show similar trends, but these results are confounded because two of the relationships are nonlinear (see Fig. 1). The distribution of the correlations of B with A approximates a normal curve centred on zero (Fig. 3a). The use of B/A shifts the distribution to a median value of -0.573, but the distribution is skewed (Fig. 3b) because of non-normality and the non-linear relationship between B/A and A (e.g. see Fig. 1b). The greatest shift in the distribution occurs with B/A and V/A where approximately 90% of the random correlations had values equal to or exceeding 0.90 (Fig. 3c). These correlations are adversely influenced by a few points which could be considered outliers (Fig. 1c). The inverse of mean depth (i.e. A/V) and B/A approximates a linear relationship, however, the expected correlations for these ratios are centred at -0.400 (Fig. 3d). The randomized correlations for the logarithmic transformation of B/A and V/A has a median value of 0.682 (although the variance of the B/A term suggests that a logarithmic transformation may not be appropriate; i.e. see Fig. 1d). Again

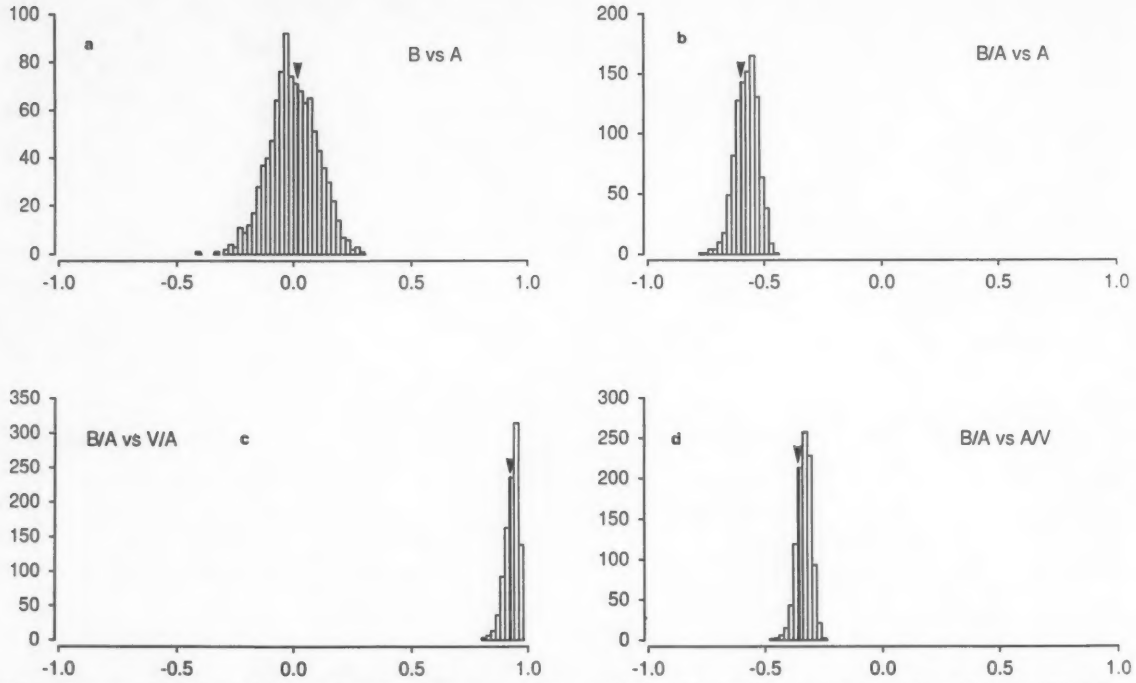

FIG. 3. Frequency distributions of Pearson product-moment correlation coefficients from 1 000 permuted correlations of the simulated data. Observed correlations from Fig. 1 are indicated by arrows.

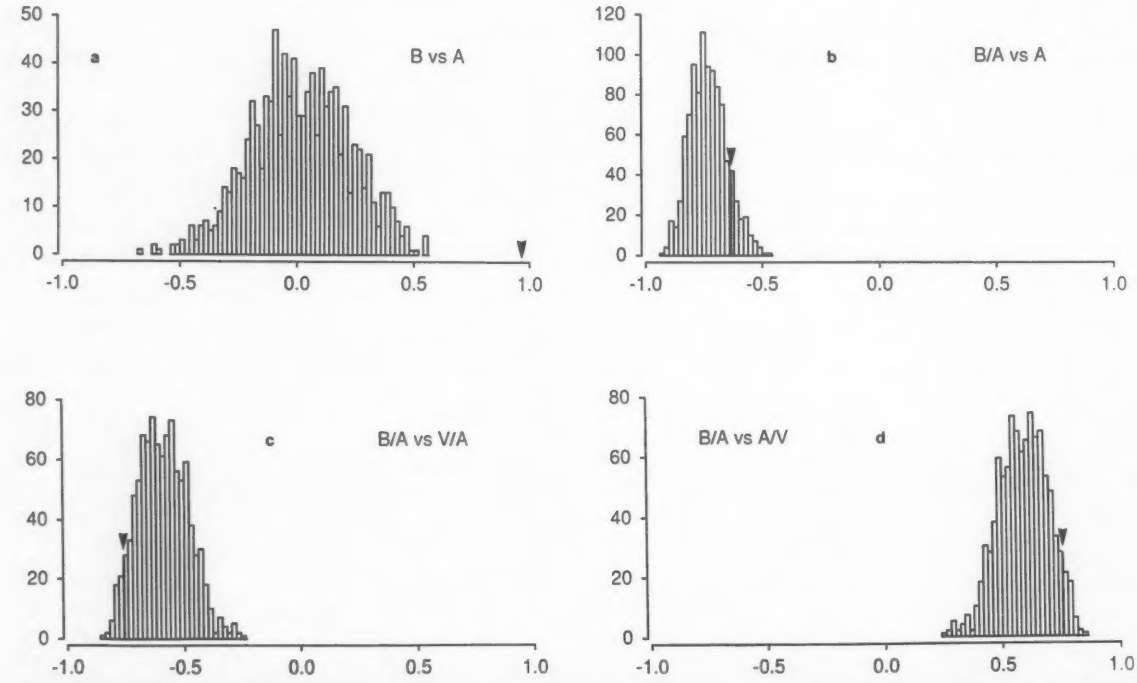

FIG. 4. Frequency distributions of Spearman rank correlation coefficients from 1 000 permuted correlations of Ryder's 'A' (1965) data. Observed correlations are indicated by arrows.

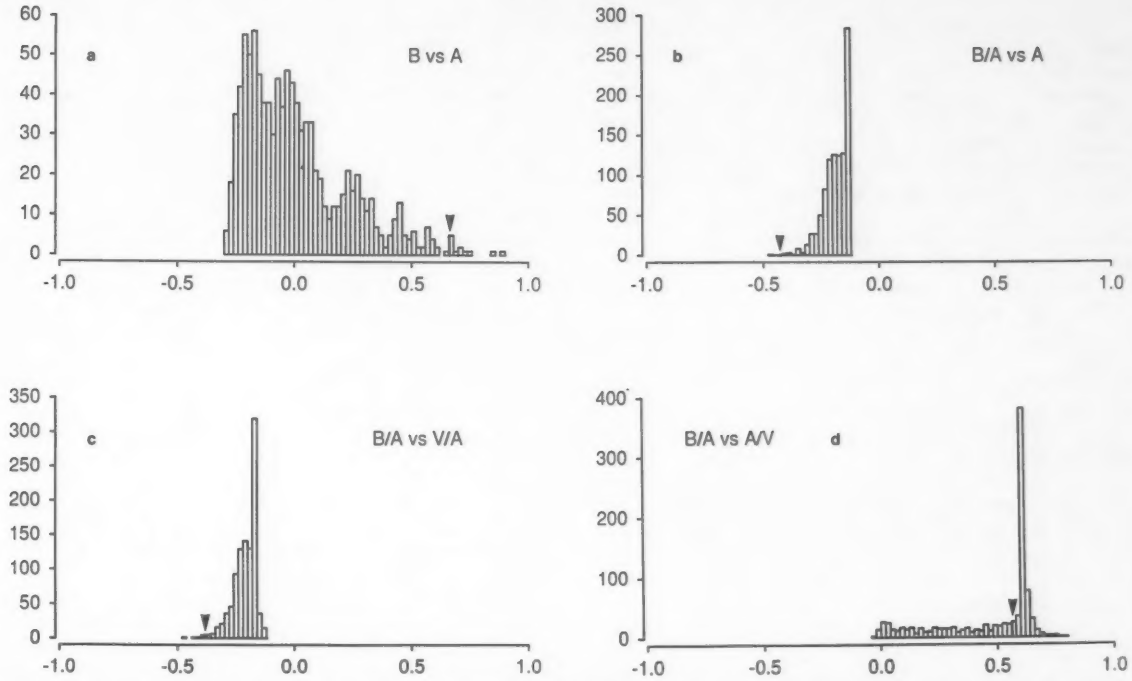

FIG. 5. Frequency distributions of Pearson product-moment correlation coefficients from 1 000 permuted correlations of Ryder's 'A' (1965) data. Observed correlations are indicated by dashed lines.

we note that the observed correlations for each relationship fall within the central region of each distribution, which differ markedly from a symmetrical distribution around zero when ratios are employed.

Published Data

We analysed Ryder's (1965; $N = 23$) data set where the MEI was proposed and confirmed the results by the analysis of additional data sets (Table 1). The observed rank correlation between B and A is highly significant ($P = 0.001$; Table 1) and did not fall within the distribution of randomized values (Fig. 4a). The standardization of biomass to a yield-per-unit-area measure (B/A) resulted in a nonsignificant correlation with lake area ($P = 0.909$; Fig. 4b). Additionally, the rank correlations between B/A and mean depth (V/A) or the inverse of mean depth (A/V) only approached the critical value of 0.05 ($P = 0.065$; Fig. 4c and 4d). As expected, identical rank correlations were obtained for the log-transformed relationships. As with the simulated data, the distribution of randomized correlations associated with ratio variables does not include 0. Unfortunately, Ryder (1965) and subsequent workers used the traditional comparison with 0 to test their observed correlations (although with the Pearson product-moment rather than Spearman rank correlations).

Randomizations for the Pearson correlations resulted in an asymmetrical distribution for B vs. A that was centred at approximately 0 (Fig. 5a). This asymmetry probably arose from the inherent non-normality of the data, but the observed correlation was large ($P = 0.004$; Table 1). Biomass per unit area (B/A) was correlated ($P = 0.001$) with both area (A; Fig. 5b) and mean depth (V/A; Fig. 5c), although Pearson correlations are inappropriate because these relationships are strongly nonlinear (i.e. compare with results from the rank correlation in Fig. 4). The relationship of B/A with the inverse of mean depth (A/V) is approximately linear, but nonsignificant ($P = 0.555$; Fig. 5d). A logarithmic transformation of mean depth (V/A) and biomass per unit area (B/A) results in a significant correlation ($P = 0.005$), but this is due to the influence of several outlying points as indicated by the corresponding nonsignificant rank correlation (see Table 1).

Rank correlations between B and A were significant for all of the 10 data sets analyzed (Table 1), but not between biomass per unit area (B/A) and lake surface area even though this relationship is reported frequently in the literature (e.g. Rawson 1952, 1961; Ryan and Kerekes 1989). Due to the multiple comparisons involved with each data set, a Bonferroni correction should be employed to maintain the overall probability at the value of 5%. This correction requires an observed significance level of $P < 0.005$ (i.e. probability level divided by the number of tests). Using this corrected probability, we find that the null hypothesis of a random rank correlation of B/A and A, mean depth (V/A) or the inverse of mean depth (A/V) cannot be rejected for any of the data sets. Although several Pearson correlations do reject the null hypothesis, these are flawed by the nonlinear nature of the data and outliers, hence violation of the assumptions associated with the use of Pearson correlation (e.g. see Fig. 1, and figures in the various cited studies).

Discussion

The advantages of mean depth and the MEI rest on their usefulness as predictors (i.e. high r^2) of plankton, benthos, and

fish biomass or production (e.g. see Ryder (1982) and Ryder et al. (1974) for reviews. Mean depth is viewed as the most useful and important single morphometric variable in limnological and fisheries science. In fact, Ryder et al. (1974) have described mean depth as a measure of euphotic zone, overall temperature regime, area of the lake suitable for aufwuchs growth, ecotone between terrestrial and aquatic zones, and ecotone between sediment and aquatic zones. Additionally, lakes with small mean depths have potentially rapid recycling of nutrients (i.e. are morphologically eutrophic) whereas deeper lakes may experience a hypolimnetic 'nutrient sink' where nutrients may be lost temporarily or permanently (i.e. morphologically oligotrophic).

All the correlated factors which Ryder et al. (1974) and Ryder (1982) have identified represent processes that are best summarized as large-scale features (i.e. whole lake, e.g. the euphotic zone). However, because total biomass in lakes is assumed to be dependent on lake size, researchers standardize biomass to provide an average biomass-per-unit-area (see Welsh et al. 1988 for a discussion of statistical shortcomings of averages). Because the factors which influence biomass in lakes are large-scale, it would be most appropriate to analyze biomass measures on a similar scale (e.g. whole-lake total biomass). Researchers wanting to remove the effects of lake size from their analyses may use a covariate (e.g. lake area) in an analysis of covariance rather than simply dividing all variables by area (e.g. see Packard and Boardman 1987, 1988).

Unfortunately, the justification for the utility of mean depth and MEI was developed post facto. Ryder et al. (1974) state that a theoretical basis for the MEI does not exist, but empirical studies have shown that the measure does work. Herein, we show that comparable results may be obtained simply by creating ratios from random, uncorrelated numbers. Thus, the high proportion of variance explained in studies using ratios like mean depth or the MEI are probably due to inflated (i.e. spurious) correlations because the ratio variables are not statistically independent $\left(\text{e.g. } \frac{B}{A}, \frac{V}{A}, \text{ see Chayes 1971}\right)$. Although mean depth, the MEI and many other ratios and indices conceptually simplify complex interrelationships, they are inappropriate in models based on inferential statistics unless the appropriate null model is considered (i..e what is the null correlation for no association?). Although problems with ratios have been identified many times (e.g. Atchley et al. 1976; Green 1986), workers often fail to identify explicitly that the null model (i.e. null correlation) of no association changes when ratio variables are formed. As Chayes (1971, page 7) states the "null value, against which a sample correlation is to be tested, however, is not the zero characteristic of the untransformed variables but the correlation found after, and *thus generated by*, the transformation" (italics are Chayes'). Although an approximation for his null correlation may be calculated using the formula of Pearson (1897), such approximations are biased if the original variables have coefficients of variation exceeding 15% (Chayes 1971). In contrast, randomization tests can be used to evaluate correlations between ratio variables whenever some of the standard statistical assumptions (e.g. random sampling) are violated.

Problems with spurious correlations usually arise from a posteriori data manipulation. Within that context, the data used to formulate the MEI were collected as total catch per lake (e.g. Rawson 1952), but subsequent hypotheses focused on standardized catch per unit area, thereby inadvertently introducing a spurious component when adjusted catch was correlated with lake area (or any correlated morphological variable). Had the original data been collected in a standardized form (i.e. a standard area fished in each lake to produce a response variable based on catch per unit area [not divided by area!]), no such spurious correlation would have occurred.

As a result, only certain types of ratio variables will yield spurious correlations. That is, data measured in a standardized form differ statistically from data that are standardized a posteriori (i.e. where inappropriate data were collected to test a desired hypothesis). As we have demonstrated above, spurious correlations between response and predictor variables will compromise statistical tests of hypotheses, including tests associated with exploratory, model-building algorithms (e.g. stepwise multiple regression). If the data and subsequent analyses are possibly biased by spurious correlations, a randomization test will correctly assess the significance of hypotheses of interest, including inter-relationships involving ratios.

Many other indices are prone to the same spurious self-correlations. For example, Ryder et al. (1974) show that the MEI resembles equations generated by Vollenweider (1968) and Schindler (1971) to model nutrient loading in aquatic systems (also see Hargrave's (1973) study of benthic respiration and primary production). Generally, biologists frequently standardize measurements by dividing by overall volume or mass to scale for size effects (e.g. oxygen consumption, carbon production, gonadosomatic index; see Leatherland and Sonstegard 1987). Such scaling adjustments often lead to spurious self-correlations (e.g. Atchley et al. 1976; Packard and Boardman 1987, 1988; Jackson and Somers 1990), but the implications of these self-correlations have been largely ignored (Kenney 1982).

We challenge the traditional use of ratios because we have demonstrated that statistical results based on ratios are prone to spurious self-correlations contributing to inflated correlations and incorrect interpretation. We advocate the use of alternative techniques such as the analysis of covariance that avoid the use of ratios or indices (e.g. see Hinch and Green 1988; Magnusson 1989; Packard and Boardman 1988, 1989; Tracy and Sugar 1989). However, if researchers must use ratios, we strongly emphasize that the correct null correlation be considered and randomization tests be used to evaluate the significance of departure from the expected null correlation.

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Sensory Mechanism and Selective Advantage for Diel Vertical Migration in Juvenile Sockeye Salmon, *Oncorhynchus nerka*

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Levy, D. A. 1990. Sensory mechanism and selective advantage for diel vertical migration in juvenile sockeye salmon, *Oncorhynchus nerka*. Can. J. Fish. Aquat. Sci. 47: 1796–1802.

Diel vertical migrations are commonly undertaken by juvenile sockeye salmon within pelagic lake nursery environments. Data from hydroacoustic surveys in British Columbia lakes are used to compare predictions from sensory mechanism and selective advantage theories for diel vertical migration with the performance of the animals under field conditions. The observations suggest that light and temperature controlled juvenile sockeye day and night depth positions respectively. A multifactor hypothesis, which interprets the migration as a three-way compromise between foraging, predator avoidance, and the optimization of nocturnal metabolic efficiency, provides the most realistic explanation for the selective advantage of the behavior.

Les saumons rouges juvéniles vivant en milieu pélagique dans des lacs d'alevinage effectuent souvent des migrations verticales nycthémérales. Des données hydroacoustiques recueillies dans des lacs de la Colombie-Britannique ont servi à comparer les prévisions formulées au moyen des théories faisant appel aux mécanismes sensoriels et à l'avantage sélectif concernant les migrations verticales nycthémérales avec le comportement réel des poissons en nature. Les observations laissent entendre que la lumière et la température régulent la position verticale des saumons rouges juvéniles dans la colonne d'eau durant le jour et la nuit respectivement. L'explication la plus juste de l'avantage sélectif de ce comportement nous est fournie par une hypothèse multifactorielle suivant laquelle cette migration serait le fruit d'un compromis entre la recherche de nourriture, l'évitement des prédateurs et l'optimisation de l'efficacité du métabolisme nocturne.

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Diel vertical migration behavior is widespread in aquatic organisms and has evolved independently in many thousands of species from at least 15 different phyla (Kerfoot 1985). Among fish, diel vertical migrations are undertaken by both pelagic and demersal species. Demersal fishes are usually near the bottom by day and tend to move off bottom and into the water column at night (Beamish 1966; Bowman and Bowman 1980). In contrast, pelagic species often complete their diel migration in the water column well away from solid structures which might serve as vertical references. There are similarities in the diel vertical migrations of pelagic species in different aquatic environments, e.g. herring (*Clupea harengus*) in the ocean (Blaxter 1985) and juvenile sockeye salmon (*Oncorhynchus nerka*) in freshwater nursery lakes (Narver 1970). Both species feed on planktonic crustacea and there are marked similarities in the vertical distance travelled, as well as in the number, timing, and duration of surface ascents. The parallel vertical migratory behavior in these two pelagic planktivores suggests that similar selective pressures may have operated on both species during the course of evolution.

An adequate explanation of diel vertical migration must specify both a sensory mechanism and a selective advantage for the behavior. For juvenile sockeye salmon, I previously hypothesized sensory mechanisms involving both light and temperature to control, respectively, the day and night vertical depth positions (Levy 1987). What selective advantages accrue to individuals which migrate compared to non-migrants (which maintain a fixed depth in the water column) or randomly distributed animals? Existing answers to this question explain the behavior in terms of zooplankton foraging success (Begg 1976; Janssen and Brandt 1980), bioenergetics (Brett 1971), and predator avoidance (Eggers 1978). The "antipredation window" hypothesis of Clark and Levy (1988) views diel vertical migration in juvenile sockeye as a compromise between zooplankton foraging success and predator avoidance

There are major differences in morphometry, biological community composition, and limnological characteristics among sockeye lakes (Foerster 1968), as well as substantial seasonal changes. These environmental and biological differences may affect the diel vertical migrations of the fish in predictable ways if there are common causal mechanisms for the behavior in different lakes. In this study, I compare the diel vertical migrations of juvenile sockeye in diverse British Columbia lakes to test the validity of sensory mechanisms hypothesized by Levy (1987) and to allow inferences to be made concerning the selective advantage of the behavior.

Study Lakes

Twelve lakes in British Columbia (Fig. 1) were studied. Limnological characteristics for most of the lakes are described by Goodlad et al. (1974), Stockner and Shortreed (1983, 1985) and Stockner (1987). Lakes were sampled when juvenile sockeye populations were relatively dense. During the period of study, large adult spawning escapements occurred within Fraser (1985), Meziadin (1985), Babine (1985), Quesnel (1985), Chilko (1986), and Shuswap (1986) lakes. These lakes were visited during the year subsequent to the occurrence of the dense spawner populations so that sampling coincided with high densities of pelagic juvenile sockeye. Okanagan Lake is dominated

FIG. 1. Location of study lakes within the province of British Columbia.

TABLE 1. Schedule of field trips to study lakes.

Babine:	Great Central:	Okanagan:
June 25–26/86	May 26–27/86	June 6–7/87
Aug. 1–2/86	July 20–21/86	July 1–2/87
Aug. 19–20/86	Sept. 6–7/86	July 21–22/87
Oct. 13–14/86		Oct. 1–2/87
Chilko:	Kennedy:	Owikeno:
July 27–28/86	May 28–29/86	Oct. 1–3/85
July 14–15/87	July 20–21/86	Sept. 11–14/86
Aug. 15–16/87	Sept. 4–5/86	
Cultus:	Meziadin:	Quesnel:
Apr. 14–16/86	June 23–24/86	Aug. 4–5/86
July 9–10/86	Aug. 10–11/86	Aug. 23–24/86
Sept. 29–30/86		Sept. 20–21/86
		Aug. 11–12/87
Fraser:	Nimpkish:	Shuswap:
June 27–28/86	June 16–17/86	Sept. 23–25/85
Aug. 21–22/86	Sept. 8–9/86	July 1–2/86
Oct. 14–15/86	Sept. 16–17/86	July 2–4/87
		July 18–20/87
		Sept. 28–29/87
		Nov. 4–5/87

by kokanee (lake-locked sockeye) and was visited during the summer and fall months of 1987. The lakes were sampled on dates shown in Table 1. Specific sampling locations are given in appendix 2 of Levy (1989).

Methods

Data on diel vertical migration of fish were collected using a hydroacoustic method. A 420 kHz BioSonics echosounder with a 15 degree transducer (−3db, full angle) was used to generate echo signals (0.4 ms pulse width at a rate of $2 \cdot s^{-1}$) which were digitized and taped on video cassette recorder (VCR) tape. The transducer was mounted on a rotatable pipe fixed to the side of a 5 m fiberglass boat.

In several of the study lakes (Babine, Chilko, Cultus, Fraser, Quesnel, Shuswap), trawling results (Narver 1970; J. Hume, Department of Fisheries and Oceans, Cultus Lake Laboratory, Cultus Lake, B.C. V0X 1H0, unpubl. data) indicate that juvenile sockeye were numerically dominant, accounting for over 90% (and frequently 100%) of trawl catches. Thus, in these lakes, hydroacoustic targets could be safely identified as juvenile sockeye. Threespine sticklebacks (*Gasterosteus aculeatus*) co-occurred with sockeye in the pelagic zones of five lakes (Great Central, Kennedy, Meziadin, Nimpkish, and Owikeno), potentially confounding the identification of acoustic targets in these lakes. Midwater trawl and surface tow-net sampling (Chernoff 1971) indicated that sticklebacks in Owikeno Lake maintained a shallower diel vertical distribution than juvenile sockeye.

The primary method of extracting information on depth distribution of fish was echo integration (Thorne 1971; Burczynski

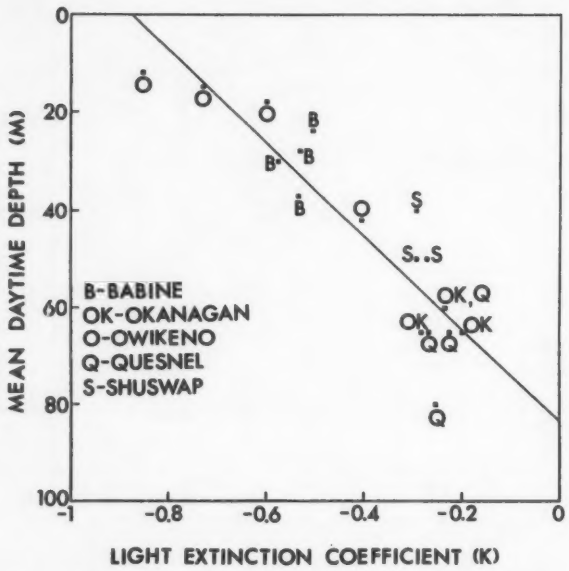

FIG. 2. Mean daytime depth of fish targets plotted against the light extinction coefficient, K, in Babine, Owikeno, Quesnel, Shuswap, and Okanagan lakes.

1982). Echo integration of the taped echo data was done in the laboratory with a BioSonics Model 121 digital Echo Integrator. Voltage thresholds during echo integration were established at 50 mV above ambient noise levels (measured with an oscilloscope). Since the objective was to monitor diel variation in relative (not absolute) fish density, a value of 1 was used for the instrument scaling factors "A" and "B." "A" is usually computed from factors derived from the hydroacoustic hardware, the velocity of sound in water, and the average back scattering cross section of the fish and has units of fish $\cdot m^{-3} \cdot V^{-2}$. "B" is a unitless scaling factor which is used to correct for deviations in the time-varied gain in the echo sounder. The echo integrator output (V^2) was then used as a measure of the relative fish biomass in different depth strata.

Mean depth, Z, of a fish population along a given transect was computed as:

$$Z = \frac{\sum_{i=1}^{m} Z_i V_i^2}{V_t}$$

where V_i^2 is the echo integrator output in depth strata i, $Vt = \sum_{i=1}^{m} V_i^2$, and m is the total number of depth strata. An alternative index of depth distribution, the depth of maximum echo integrator voltage, was used for analysis of juvenile sockeye depth preference when other types of fish targets were numerous in the transducer beam. The latter index provided a more accurate estimate of juvenile sockeye depth position than the mean depth in mixed species situations.

A hand-operated winch system with a 5 kg weight was employed to position temperature and light sensors accurately in the water column. Temperature measurements were taken with a YSI-SCT meter at mid-day, at 1 m depth intervals from the surface down to 50 m. Surface temperatures were also measured with a mercury thermometer, accurate to 0.1°C, to derive a correction factor (usually less than 0.5°C) which was applied to the vertical temperature profile. Light profiles were measured near mid-day during periods of constant atmospheric radiation. Light was measured in microeinsteins (1 microeinstein $= 6.02 \times 10^{17}$ photons; 1 lux $= 5.17 \times 10^{6}$ photons $\cdot m^{-2} \cdot s^{-1}$) using a Li-Cor 185-A Quantum meter with an underwater quantum sensor. Measurements were taken at 1 m intervals from the surface down to a depth corresponding to the minimum sensitivity of the sensor. Light extinction coefficients, K, were estimated by fitting regression lines to the standard formula for exponential light extinction (Wetzel 1983):

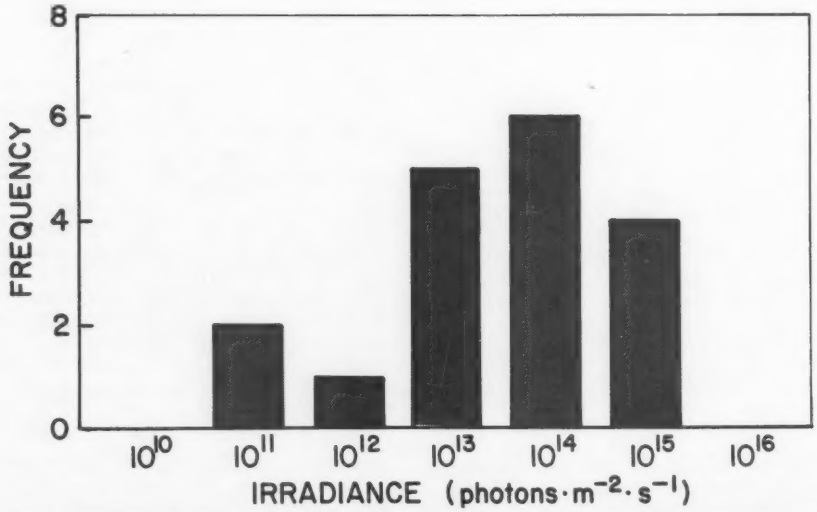

FIG. 3. Frequency distribution of calculated light intensities at the daytime depth of maximum fish biomass.

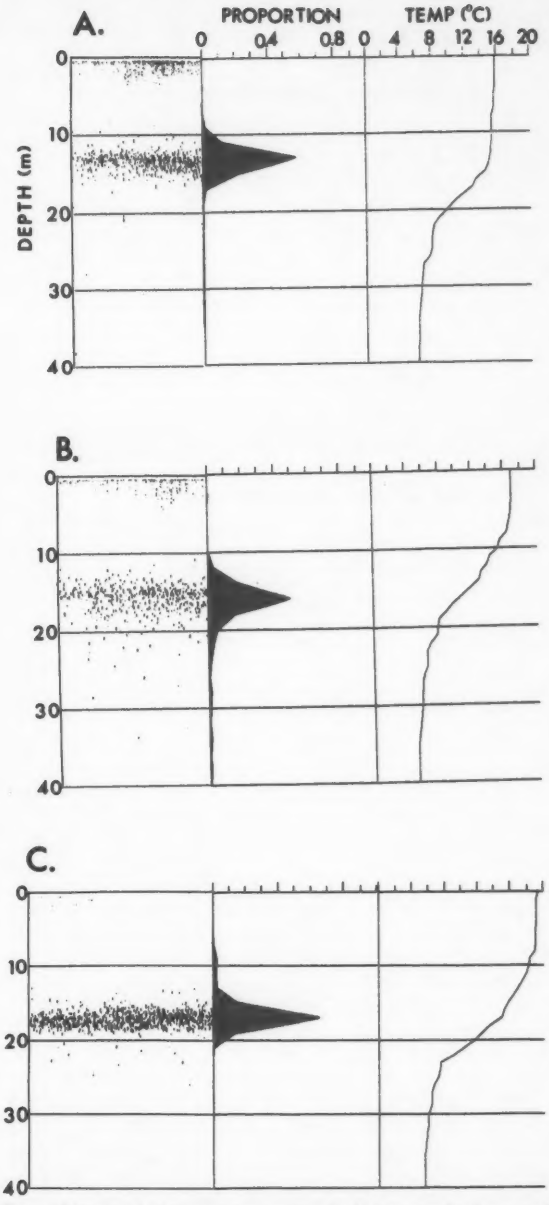

FIG. 4. Nocturnal echogram, proportion of echointegrated voltage, and temperature profiles for (A) Babine Lake on Aug. 20, 1986, (B) Quesnel Lake on Aug. 23, 1986, and (C) Shuswap Lake on July 18, 1987.

$$I_d = I_o e^{-Kd}$$

where I_d is the measured illuminance at depth, d.

Results

To compare mean daytime depth of juvenile sockeye with water clarity conditions, I considered only deep lakes where the presence of a lake bottom did not interfere with the daytime descent of the fish. In shallow lakes (e.g. Cultus and Fraser) sockeye daytime descents could be constrained by the presence of the lake bottom. There was a significant relationship between water clarity and the daytime depth of juvenile sockeye (Fig. 2). Sockeye in transparent lakes (e.g. Quesnel and Shuswap) occupied deeper positions in the water column than did sockeye in more turbid lakes. The following regression relating fish depth and light extinction coefficient was obtained:

$$\text{Depth} = -15.4\,K^{-1} - 1.23 \qquad (r^2 = 0.83;\ P < 0.05)$$

where K is the light extinction coefficient. These observations are consistent with the hypothesis that sockeye daytime depth distribution is influenced by water clarity conditions.

During daylight peiods, juvenile sockeye were distributed at depths with extremely low light levels (Fig. 3) where they experienced a mean irradiance level of 1.1×10^{15} photons $\cdot m^{-2} \cdot s^{-1}$ (range $= 10^{11} - 10^{16}$ photons $\cdot m^{-2} \cdot s^{-1}$).

At night, juvenile sockeye occupied discrete depth positions within the water column (Fig. 4). Nocturnal vertical distribution evidently reflected thermoselection behavior since most fish were situated at, or near, the thermocline (Fig. 4). As the summer progressed, they shifted downward in the water column (Fig. 5). In Babine Lake on June 25, sockeye occupied shallow depths at night and the absence of echo targets on the echogram was due to a nocturnal surface orientation on this date. During August they occupied depths of 5–15 m at night, and moved down to mainly between 10 and 20 m depth in October (Fig. 5).

The nocturnal temperature preference of juvenile sockeye was measured first by echo integrating nocturnal transects and establishing the depth of maximum echo integrator voltage. The temperature at this depth was then extrapolated from the temperature profile to obtain a distribution of temperatures associated with the maximum fish biomass (Fig. 6A). The distribution of preferred nocturnal temperatures was centred around a mean of 10.9°C, slightly higher than the mean of 9.2°C for Lake Washington (Woodey 1972), and somewhat lower than the preferred 12–15°C which occurs in laboratory-induced vertical temperature gradients (Brett 1952). Since the thermocline in most temperate, stratified lakes occupies a relatively narrow depth range compared to the depth ranges of the hypolimnion and epilimnion, the relatively narrow distribution of preferred nocturnal temperatures (compared to the range of temperatures available in the entire water column) is consistent with a nocturnal thermoselection mechanism.

Discussion

Sensory Mechanism

Sensory mechanisms controlling vertical migration of juvenile sockeye should account for day and night depth positions as well as the diel timing of their migration. Observations from B.C. sockeye lakes indicate sensory mechanisms involving both light response and thermoselection to control the day and night time depth positions respectively.

Preferred daytime depth was related to water clarity. Sockeye juveniles in clear lakes tended to be deeper and to migrate over greater vertical distances than those in turbid lakes. During nocturnal periods, juvenile sockeye were evidently thermoselective and were found within a relatively narrow range of temperatures. For ectothermic organisms in thermally stratified lakes, temperature can provide a clear and unambiguous environmental signal. Within steep experimental

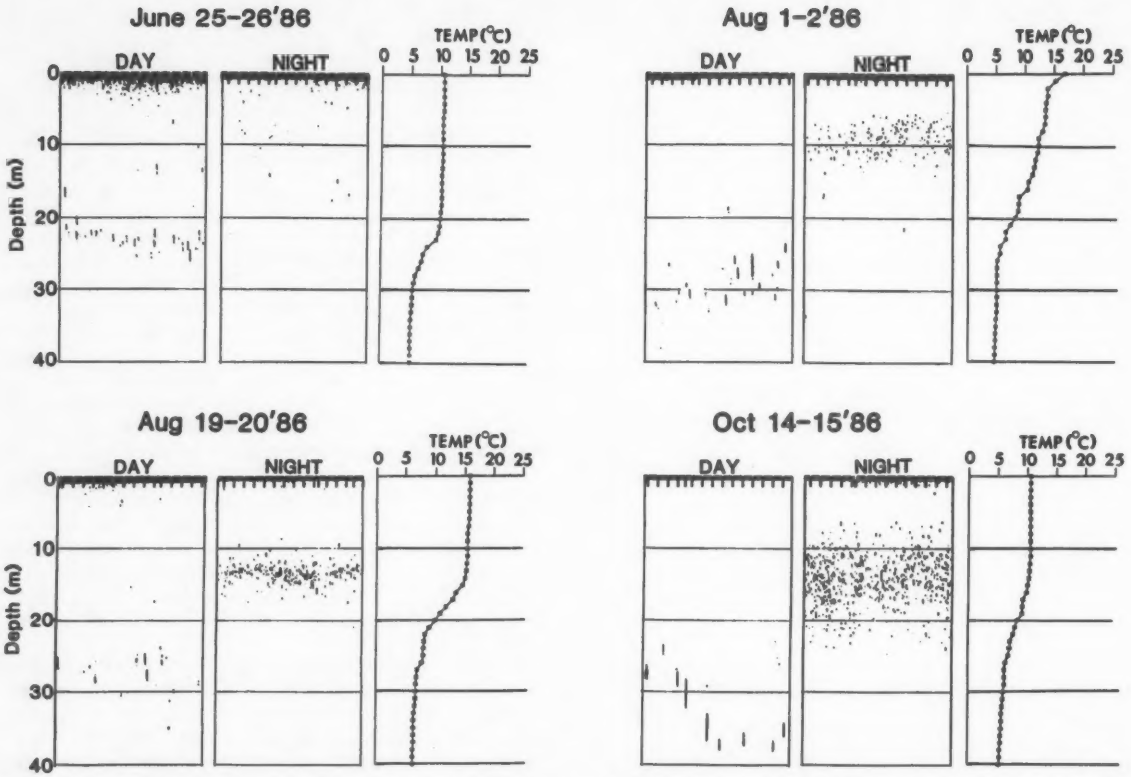

FIG. 5. Day and night echograms from Babine Lake, 1986, shown in relation to the temperature profiles. Ticks on echograms depict 1 min time intervals.

gradients of temperature in the laboratory, most fish show strongly peaked, monomodal frequency distributions (Neill 1979).

Two different mechanisms capable of controlling the diel timing of fish vertical migrations were elaborated by Blaxter (1974). The first involved the fish "following isolumes" whereby the animals remained within a distinct light intensity preferendum, while the second was a function of the fish responding to a specific rate of change in light intensity. Both of these mechanisms would result in crepuscular migration. In a review of photoperiodically-induced shifts on animal behavior, McFarland (1986) concluded that the influence of light upon diel shifts in animal activity was poorly understood for most aquatic species. The crepuscular timing of diel vertical migration suggests a role for light in controlling the vertical migration of juvenile sockeye. The particular attributes of light to which the fish respond, however, are difficult to specify.

The potential usefulness of the diel cycle as an orienting mechanism in fish behavior was summarized by Smith (1985). Other vertical migrators respond directly to light intensity (Woodhead 1966; Blaxter 1974) and can be affected by solar eclipses (Backus et al. 1965), artificial lights (Blaxter and Currie 1967), and the absence of darkness during polar summers, which may inhibit vertical migration altogether (Zusser 1958, cited in Blaxter 1974).

Alternative sensory mechanisms capable, in theory, of controlling juvenile sockeye diel depth distribution include (1) a diel shift in temperature preference, and (2) a diel shift in pressure sensitivity. Both of these mechanisms need to be coupled with light in order to account for the diel timing of migration. Some fish species have diel thermoregulatory rhythms (Reynolds and Casterlin 1979). Most diel changes in temperature preference, however, are only a few °C, far less than the magnitude of diel temperature difference experienced by most juvenile sockeye vertical migrants (Fig. 6C). Fish with swimbladders are sensitive to pressure differences (Blaxter 1979) because of pressure-operated stretch receptors on the wall of the swimbladder (Qutob 1962). However, the observed seasonal variations in juvenile sockeye day and night depth position (Fig. 5) are difficult to reconcile with a sensory mechanism involving pressure differences, since pressure regimes within lakes should not vary seasonally.

Selective Advantage

Three single factor hypotheses which specify a selective advantage for diel vertical migration (foraging efficiency, bioenergetics, and predator avoidance) was critically evaluated by Levy (1987). A foraging hypothesis was rejected because of discrepancies in diel distribution patterns of zooplankton and juvenile sockeye. Levy (1990) confirms that zooplankton and juvenile sockeye are spatially segregated over much of the diel cycle, thereby rendering the hypothesis invalid.

The bioenergetic hypothesis (Brett 1971) is based on the idea that vertical migrants can achieve temperature-related metabolic benefits which serve to increase growth rate. This hypoth-

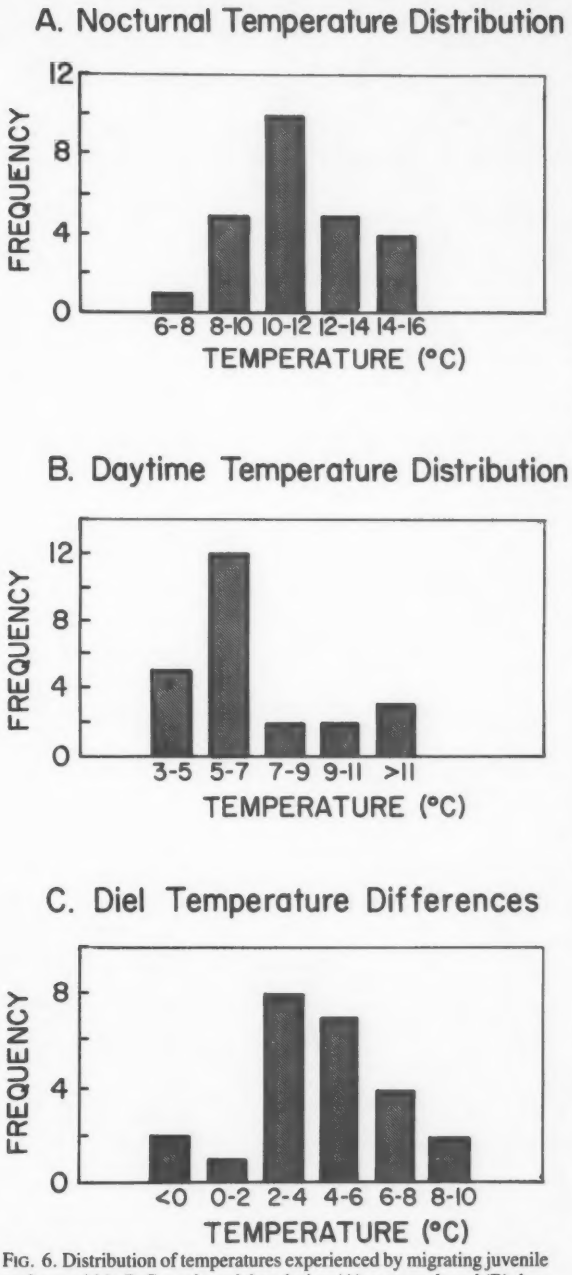

FIG. 6. Distribution of temperatures experienced by migrating juvenile sockeye within B.C. sockeye lakes during (A) nocturnal, and (B) daytime periods. Diel temperature difference experienced by vertical migrant indicated on distribution C.

esis requires that juvenile sockeye migrants experience substantially lower temperatures during daylight (non-feeding) periods in order to reduce their metabolic rate. Comparison of the temperatures experienced by juvenile sockeye migrants (Fig. 6) indicated modest (mean = 3.9°C) diel temperature differences in most lakes. This magnitude of diel temperature variation would only cause minor effects on juvenile sockeye growth rate (Brett et al. 1969). Juvenile sockeye experienced warmer temperatures by day than at night at Nimpkish Lake where vertical migrations were periodically reversed (Levy 1990). Juvenile sockeye during the present study at times migrated vertically under near isothermal conditions (Fig. 5 — June 25–26, 1986 in Babine Lake) when temperature-related bioenergetic benefits were negligible or absent. Thus it is unlikely that the bioenergetic hypothesis, in its present form, is capable of adequately explaining the selective advantage of diel vertical migrations in juvenile sockeye.

The predator avoidance hypothesis (Eggers 1978) predicts that vertically migrating juvenile sockeye will seek out isolumes where visual searching ability of the dominant piscivores is reduced or negligible. The evolved light preference of vertical migrants should therefore occur below the saturation irradiance threshold (SIT) of the dominant piscivore, where SIT is defined as the minimum irradiance that maximizes reaction distance to prey targets (Henderson and Northcote 1985). Observations from B.C. sockeye lakes (Fig. 3) are consistent with this prediction: juvenile sockeye are associated with irradiance levels that are well below the SIT values for both cutthroat trout and Dolly Varden (Henderson and Northcote 1985), two piscivores which consume juvenile sockeye in the pelagic zone (Ricker 1941).

The predator avoidance hypothesis is attractive as a simple way to account for the diel timing of vertical migration by juvenile sockeye. This hypothesis was extended by Clark and Levy (1988) to explicitly consider the trade-off between zooplankton food intake and predation risk within the euphotic zone, since both juvenile sockeye and their piscivorous predators rely primarily on vision for prey search. Clark and Levy (1988) assumed a sigmoid-shaped functional relationship between feeding rate and visual sighting range underwater. The model predicts a displacement between the sockeye feeding rate curve (sockeye feeding on zooplankton) and mortality rate curve (piscivores feeding on sockeye) such that the ratio of mortality risk to feeding rate for juvenile sockeye is minimized at low-intermediate levels of light intensity which occur at dusk and dawn. The existence of this "antipredation window" would provide a strong selective pressure for sockeye to migrate into shallow surface waters for brief crepuscular periods.

The antipredation window hypothesis successfully predicts the timing and duration of juvenile sockeye vertical feeding excursions into shallow surface waters. However, the model does not predict any specific nocturnal migration pattern. At light levels below the visual feeding thresholds of sockeye and their predators, a combined antipredation window and bioenergetic hypothesis predicts a nocturnal occupation of the thermocline where temperatures optimize metabolic efficiency. The optimal metabolic temperature for juvenile sockeye (and probably most ectotherms) is dependent upon ration size (Brett et al. 1969). On relatively low ration sizes, maximum net growth efficiency occurs between 8–10°C (Brett et al. 1969). At night, juvenile sockeye are, in fact, associated with temperatures close to these values (Fig. 6A).

Wurtsbaugh and Neverman (1988) demonstrated that in Bear Lake, Utah — Idaho, the sculpin, *Cottus extensus*, derived energetic benefits from diel vertical migration. The animals migrated from the 4–5°C lake bottom, where they fed upon benthic ostracods and copepods by day, into the thermocline region of the water column at night, concentrating at temperatures between 13–16°C. Data from growth experiments sug-

gest that these temperatures served to stimulate digestion rates, thereby increasing feeding and growth rates. Nocturnal association with temperatures optimal for juvenile sockeye growth is not incompatible with an antipredation window hypothesis. Provided that light levels are beneath the visual feeding thresholds of sockeye and their predators, nocturnal association with temperatures that optimize growth would benefit a food-limited ectotherm. Thus foraging, predator avoidance, and bioenergetic factors may all combine to provide the selective advantage for diel vertical migration in juvenile sockeye salmon.

During daytime periods, a combined antipredation window — bioenergetic hypothesis predicts a juvenile sockeye descent into the hypolimnion (which would occur at the expense of metabolic efficiency) for concealment from pelagic, visual-feeding piscivores. Viewed from this perspective, diel vertical migration by juvenile sockeye would reflect a three-way compromise between foraging, predator avoidance, and metabolic efficiency. This hypothesis has yet to be formalized within a numerical model but it provides a reasonable explanation for the selective advantage of diel vertical migration behavior in juvenile sockeye. Future empirical studies are required to quantify the three-way trade-off between foraging, predator avoidance, and bioenergetics.

Acknowledgements

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Reproductive Homing in Muskellunge, *Esox masquinongy*

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Crossman, E. J. 1990. Reproductive homing in muskellunge, *Esox masquinongy*. Can. J. Fish. Aquat. Sci. 47: 1803–1812.

The number and nature of muskellunge moving to and from spawning grounds are extensively documented. Individual spawning muskellunge in Stony Lake, Ontario are considered to home annually to specific spawning grounds and to specific areas (spawning sites) within spawning grounds. Some individuals were caught in the same location, or a nearby location, in as many as 7 yr. There is some evidence for discrete populations with apparent reproductive isolation and no interchange in summer. Dispersal from spawning grounds to summer home ranges seems to be limited in regard to direction and area of the lake. Recapture of fish on spawning grounds suggests an obligatory return to a limited number of "traditional" spawning grounds and may extend our knowledge of the groups of fishes exhibiting this type of directed movement. The results also have serious implications for muskellunge in regard to management, shoreline development, and genetic contamination by fish culture activities.

Le nombre et la nature des déplacements des maskinongés vers les frayères et en provenance de celles-ci sont très étayés. On considère que chaque maskinongé géniteur du lac Stony (Ontario) revient chaque année à des frayères spécifiques et dans des zones spécifiques (lieux de fraye) dans les frayères. Quelques spécimens ont été capturés au même endroit, ou à proximité, pendant 7 ans. D'après des indications, il y aurait des populations particulières (discrètes) qui apparemment seraient isolées au moment de la reproduction et qui ne se mélangeraient pas pendant l'été. L'éloignement des frayères vers les aires de distribution estivale semble être limité par rapport à la direction et à la zone du lac. Il semble, d'après la recapture des poissons dans les frayères, qu'il y ait un retour obligatoire à un nombre limité de frayères "traditionnelles" et que nos connaissances des groupes de poissons présentant ce type de déplacement orienté pourraient être accrues. Les résultats ont aussi des répercussions graves sur les maskinongés relativement à la gestion, au développement du littoral et à la contamination génétique par les activités d'aquiculture.

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Considerable and long standing interest in the movements, migration, and homing of fishes has been the subject of extensive reviews (e.g. Hardin–Jones 1968; Malinin 1969; Schmidt–Koenig 1975; Baker 1978; Northcote 1978; McKeown 1984; Smith 1985; and Dodson 1988). Homing has been defined in a number of ways. Gerking's (1959:1) was simply "the return to a place formerly occupied instead of going to other equally probable places." Hardin–Jones (1968) suggested he preferred that of Heap, who defined the home as the place selected for the production and rearing of the young and the movement to it as gametic migration. That of Smith (1985:1), was "adaptive long distance movements that occur predictably in the life cycle of a species," and is the one adopted here. Interest was largely centered on those groups in which these behaviours are most prominent (e.g. Salmonidae, Clupeidae, and Anguillidae). In contrast, it seems to have been assumed they did not occur in other groups, and consequently were not looked for. Many freshwater fishes, including those in the family Esocidae, fell into that category.

Fragmentary information on these phenomena in esocids did exist. Most of it was derived from the pike (or northern pike), *Esox lucius*. It was suggested that they returned to identifiable spawning grounds year after year (Carbine and Applegate 1948; Oehmcke et al. 1958; Frost and Kipling 1967; Kaukoranta and Lind 1975; Bregazzi and Kennedy 1980; Müller 1982, 1987). Straying from spawning grounds was said to occur (Carbine and Applegate 1948; Miller 1948). Some evidence was provided for dispersal from spawning grounds to a summer home range (Carbine and Applegate 1948) and for return to a specific location even after dislocation (Crossman 1956; Halme 1957).

More precise information on movements of esocids arose from electronic tracking. Crossman (1977) demonstrated the return of displaced muskellunge and suggested they might return to a distant summer home range after spawning. Minor and Crossman (1978), Dombeck (1979), and Minor (1981) provided details on the directed nature of increased movements in late winter immediately prior to a sudden departure, eventual arrival on a spawning ground (reproductive homing?), and return later to a previously occupied summer home range (homing). Strand (1986) noted seasonal movements in relation to spawning grounds. Miller and Menzel (1986) briefly discussed reproductive and non-reproductive homing.

Although by 1977 there was a strong suggestion that groups of muskellunge returned regularly to a single spawning ground (reproductive homing), nowhere was it stated that individual muskellunge did so, or that individuals spawned every year. This led to the interest in evidence of annual use of a specific ground by individual adults and of precision of return to a specific site within a larger ground. An opportunity was provided by nets set every spring to obtain eggs and sperm for muskellunge culture. The return of fish marked and released during that activity could be followed for several years to provide

information pertinent to the existence, and accuracy, of reproductive homing. It was, however, impossible for me to alter the existing situation in ways that might have provided data adequate for a rigorous test of hypotheses.

Throughout, the term "Spawning Ground" will be applied to a larger area used for spawning (e.g. 189 ha surface area of Dunford Bay in Fig. 2 and 3). "Spawning Site" will be used for a smaller area within a spawning ground represented here by the location of a single net or a group of adjacent nets. "Spawning Season" must now be said to refer to the period of spawning activity of that year during which the nets were operated. The period covered by netting may have constituted only the first of two periods in that year when spawners were using that spawning ground. The concept of the muskellunge as a multiple spawner (Lebeau 1983) was not known during the early phase of this project. The term "New Fish" will refer to unmarked muskellunge (no tag or detectable scar). In 1978, 1980, and 1981 all new fish were tagged and released at the capture net. "Recapture" refers to any subsequent contact with a tagged muskellunge in the year of marking or subsequent years. For most considerations, recapture will be limited to the first contact in any one year. "Net of Origin" will be used for the location of capture of a new fish and the reference point for the history of that individual. This was done with the full understanding that that individual may, or may not, have used that site in the year(s) prior to marking. The definition of migration used here is that of Smith (1985, above). "Reproductive Homing," as used here, will refer to a class of migration resulting in the adult returning to a location in which it has previously spawned. Homing to natal grounds is not implied nor was it possible to test for it over the period of the study.

Study Site

Stony Lake (44°40′N × 78°20′W) is a eutrophic lake in the northeastern section of the Kawartha Lakes in central southern Ontario (Fig. 1). It contains a typical cool-water community of fishes including an "allotopic" (re other esocids) population of muskellunge. The surface area is approximately 3 725 ha, the mean depth 12.5 m, and 48% of the lake is less than 3 m deep. Fifty percent of the vegetative cover in the aquatic habitat is submergent plants characteristic of an esocid-percid-centrarchid community.

The major study area was a large bay (Dunford Bay) (189 ha) in the northwest corner of the lake (Fig. 2), a known spawning area for muskellunge. For comparison, nets were set at a second site, a suspected spawning ground at the extreme east end of the lake, approximately 12 km from Dunford Bay (Fig. 3). In 1980 this site consisted of South Bay (Fig. 2 and 3). In 1981 the secondary area was increased to include Hull Bay, 1.5 km NNW of the South Bay site. General characteristics of all sites were similar.

An attempt was made to identify other known or suspected muskellunge spawning sites around the lake (Fig. 3). Available gear and manpower made it possible to mark and recapture fish at only Dunford Bay and one additional site. With this limitation, I chose to test the extreme case with South and Hull bays, as opposed to a site adjacent to Dunford Bay.

Methods

Nets have been set annually in the same locations in Dunford Bay since 1951 to harvest eggs and sperm for hatchery culture of muskellunge. These are pound nets with cribs approximately 3.6 m^2, 2.7 m deep, set in 2 m of water. Each of the nine nets (or sites) was assigned a number (Fig. 2) which was used in all records during the study. The nets are set each year when the surface water temperature reaches 7°C, and removed when three million eggs have been acquired or when very few ripe muskellunge are captured. The period fished varies yearly from 6 to 24 d, and between 1982–86 averaged 10 d.

In 1980, four trap nets (2 m) were set in a location in South Bay that appeared to have good potential for muskellunge spawning (Fig. 2). In 1981, four trap nets were set in the 1980 locations and three nets (2 m) were set in Hull Bay. The purpose of the additional spawning ground was to test for movement from one site to another as suggested for *E. lucius* by Miller (1948).

Approximate water distances between adjacent net sites in Dunford Bay were as follows: 1 and 2 — 260 m, 2 and 3 — 460 m, 3 and 4 — 460 m, 4 and 5 — 520 m, 5 and 7 — 1 km, 6 and 7 — 430 m, 7 and 8 — 1.6 km, 8 and 9 — 975 m, and 9 and 1 — 790 m. The net sites in South Bay were approximately 150 m apart, those in Hull Bay 210 m and 540 m, and the centre of the sites in South Bay was 1.7 km from the centre of the Hull Bay sites.

At Dunford Bay, nets were lifted daily by the spawn-taking crew and adult muskellunge returned to each net after their work was completed. The research crew followed the spawning crew, removed the fish, anaesthetized each new fish in MS222, and marked it by attaching a numbered, Floy spaghetti tag at the origin of the dorsal fin. During anaesthesia vital statistics — fork length (FL) in mm, weight in g, and sex (by visible gametes) — were recorded for all new fish from each net each day and scales taken for age determination. The tag number of each recaptured fish was recorded, an attempt made to determine or corroborate sex, and the fish released immediately. After each new fish had regained equilibrium in fresh water it was released at the capture net (net of origin).

This procedure was followed at South and Hull bays except that the fish there were handled by the research crew only.

On some days in 1978, female fish in the nets in Dunford Bay were released before the research crew had an opportunity to tag them. In 1979 spawning occurred before a research crew was available.

Each year, notices were sent to resorts on the lake and placed in local newspapers requesting that anglers record the location of capture of tagged fish and release them. An accurate chart of the lake was provided on which the angler could indicate the exact location of capture, and capture information.

Age is expressed here as the number of complete annuli (Calendar Age).

The original capture (time of tagging) of a fish was used to establish "net of origin" for comparison with location of later recaptures.

Results

Data presented here were acquired over the years 1978–86. The research crew tagged fish in 1978, 1980, and 1981 and recorded recaptures in 1980 and 1981. Recaptures were recorded by the spawn-taking crew in 1979 and in 1982–86. No muskellunge were tagged in 1979 nor after 1981.

Reference will be made to results in two time periods — (1) the intensive period (1978-1983), and (2) the extended period (1978–86) which includes three additional years of

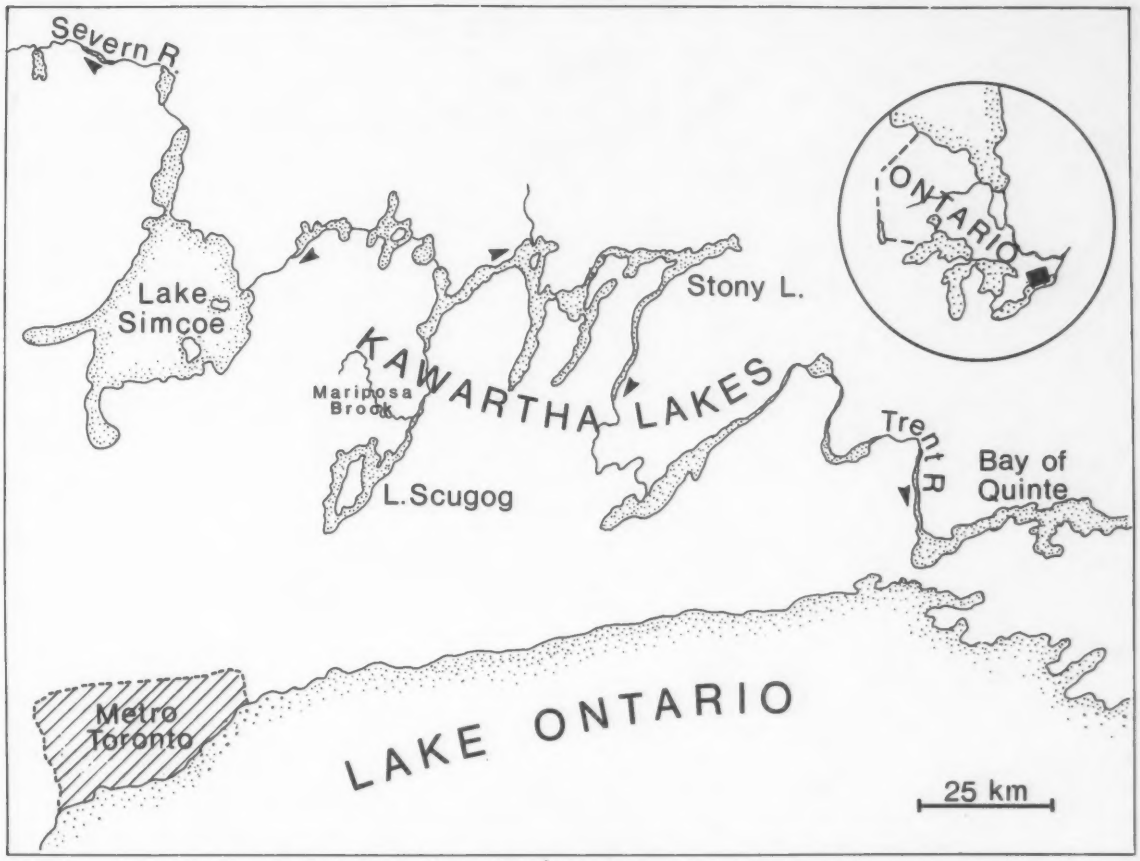

FIG. 1. Geographic area of the study. Arrows indicate the flow of two systems now connected by a canal.

information on marked fish recorded for Dunford Bay and from angled fish.

Number of Muskellunge Seen and Tagged on the Spawning Grounds

The crudest measure of reproductive homing is the recapture on a spawning ground of individuals observed previously on that spawning ground. Recapture here is limited to the first contact with an individual in any one spawning season. Some were caught several times on the same ground in one season.

From 1978 to 1986, 3 455 muskellunge were handled (new fish + recaptures) in Dunford, South, and Hull bays (Table 1). From 1978 to 1981 667 new fish were marked, recorded, and released at the net of origin. Of these, 616 were marked in Dunford Bay (West end) and 51 in South and Hull bays (East end).

Field observations indicated that mortality resulting from tagging and handling was not a problem in the study; only three such mortalities were recorded.

Age of Muskellunge Tagged on the Spawning Grounds

Of all the muskellunge caught in Dunford Bay between 1978 and 1986, scale ages were determined for 460. Age ranged from 2 to 17, modal age was 5 (n = 112) with age 6 next most frequent (n = 106), 84.9% of the individuals caught were in age-classes 5–17, and 15.1% in age-classes 2–4. Ages were determined for 264 new fish. Range was 2–11 yr, modal age was 5 (n = 74), with age 6 (n = 66) next most frequent, 83.8% fell in ages 5–11 and 36.3% in 2–4.

Considering only new fish, there were 63 captured on the Dunford Bay spawning ground which were 2–4 yr of age. Of these, 56 were captured in 1978, three in 1980, and four in 1981. The single age-2 fish was a female. There were 24 age-3 fish; 21 were males and three could not be sexed. Of the 38 age-4 muskellunge, four were female, 31 male, and three could not be aged.

Recapture of Tagged Fish on the Spawning Grounds

In the spawning seasons of 1981–86, none of the 51 muskellunge marked on the east spawning ground(s) (South and Hull bays) was recaptured on the west end ground (Dunford Bay). In 1980 and 1981, none of the 464 individuals marked by that time at the west end was recaptured on the east end ground(s).

From 1979 to 1986, 205 marked muskellunge were recaptured on the spawning grounds, 202 in Dunford Bay and 3 (in 1981) in South Bay (Table 1).

Recapture figures used here can be considered to be at minimum levels. Fish without tags but with identifiable tag scars

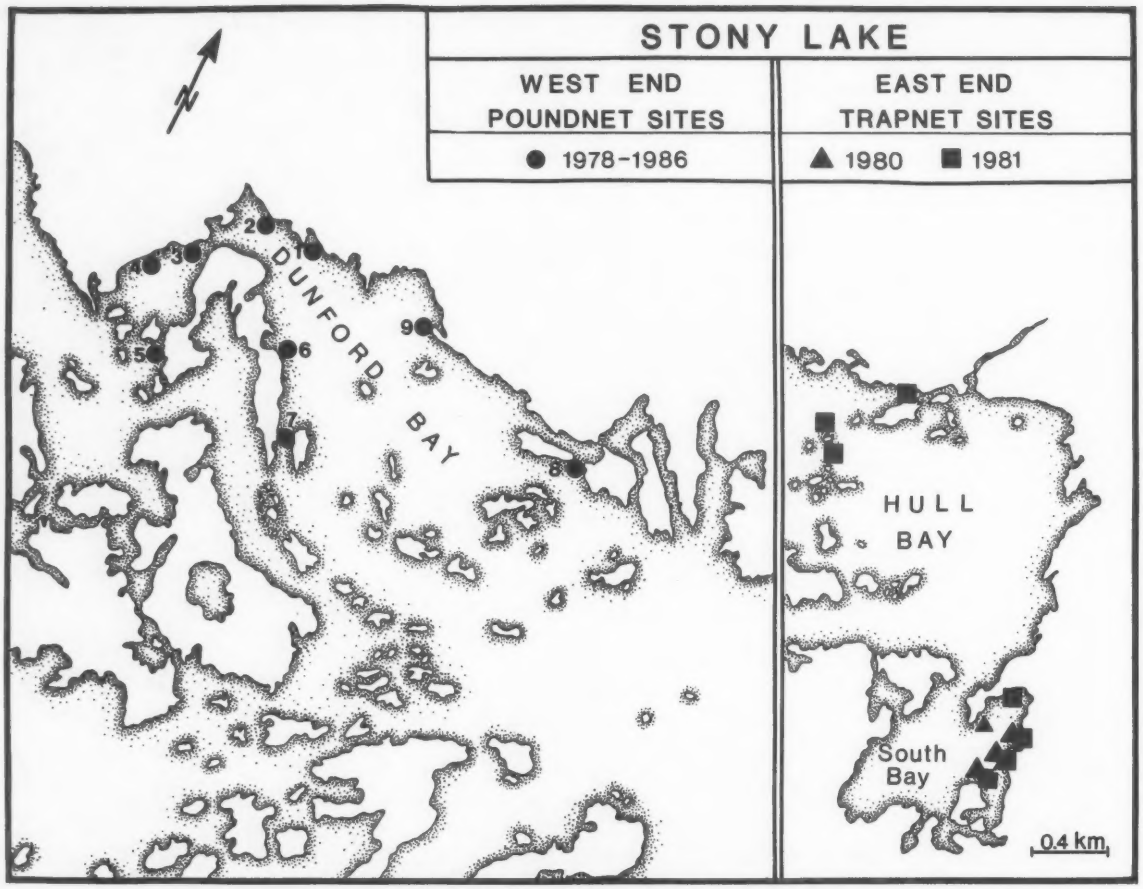

FIG. 2. Detail of location of nets in Dunford, Hull and South bays, Stony Lake. Scale bar applies to both panels.

began to appear in 1982. These scars were recorded ($\bar{x}$/yr 1982–85 = 6.8) but not used as recaptures since net of origin was not known. In addition, by 1982 there may have been tag scars on muskellunge marked for another project.

The three fish recaptured in South Bay in 1981 represent a return of 27.3% of the 11 fish marked there in 1980. The return rate to Dunford Bay spawning ground over the whole of the extended data period (1979–86) involved 616 marked fish and 202 recaptured, or 32.8%.

In 1978, 268 fish were marked on the Dunford Bay spawning ground. In 1979, 56 of them were captured there, which represents a return of 20.9% after 1 yr. In 1980, after 2 yr at large, 15 (5.6%) of the 268 individuals tagged on the Dunford Bay spawning ground in 1978 were recaptured there. After the first year, the number of marked fish at large was being reduced at an unknown rate by natural mortality, tag loss, and by a small angler harvest. Without compensating for these losses, the annual rates of return of marked fish (no. marked fish recaptured that season ÷ no. marked fish at large at start of that season × 100) would have been as follows: 1980 — 5.6%, 1981 — 6.7%, 1982 — 8.4%, 1983 — 3.6%, 1984 — 1.5%, 1985 — 1.9%, and 1986 — 0.8%.

Over the extended period of records (1978–86), individual muskellunge of Dunford Bay origin were recaptured on the Dunford Bay spawning ground one to six times in the years following marking. The numbers (and in brackets the percentage of total no. marked) were as follows: once — 99 (16.1), twice — 22 (3.6), three times — 7 (1.2), four times — 5 (0.8), five times — 2 (0.3), and six times — 1 (0.2). Most recaptures were in the year following marking, but in some instances first recapture followed tagging by as many as 5 yr. Of the 268 fish marked in 1978, 40 (14.9%) were recaptured only in 1979, five (3.7%) in 1979 and 1980, and one in 1979, 1980, and 1981. As many as six (2.2%) were recaptured first only in 1982, and exclusively single-year recaptures ended in 1983. However, a further 11 individuals (4.1%) were recaptured in nine combinations of 2–6 different yr, including 1986 (two fish). There were 15 individuals recaptured three or more times in different years (Table 2). Individuals were recaptured repeatedly not only in the same (home) spawning ground, but also in the net of origin, or an adjacent net.

Of 22 fish marked in 1978 which were captured two or more times within one spawning season, 16 were captured in the same net or an adjacent net. The extremes were records of capture in nets 3 and 9, and in nets 5 and 7 (see Fig. 2). The longest intervals between original capture and recapture on the same spawning ground in the same year were 18 and 20 d. The usual interval for repeated capture in 1 yr was 1–5 d.

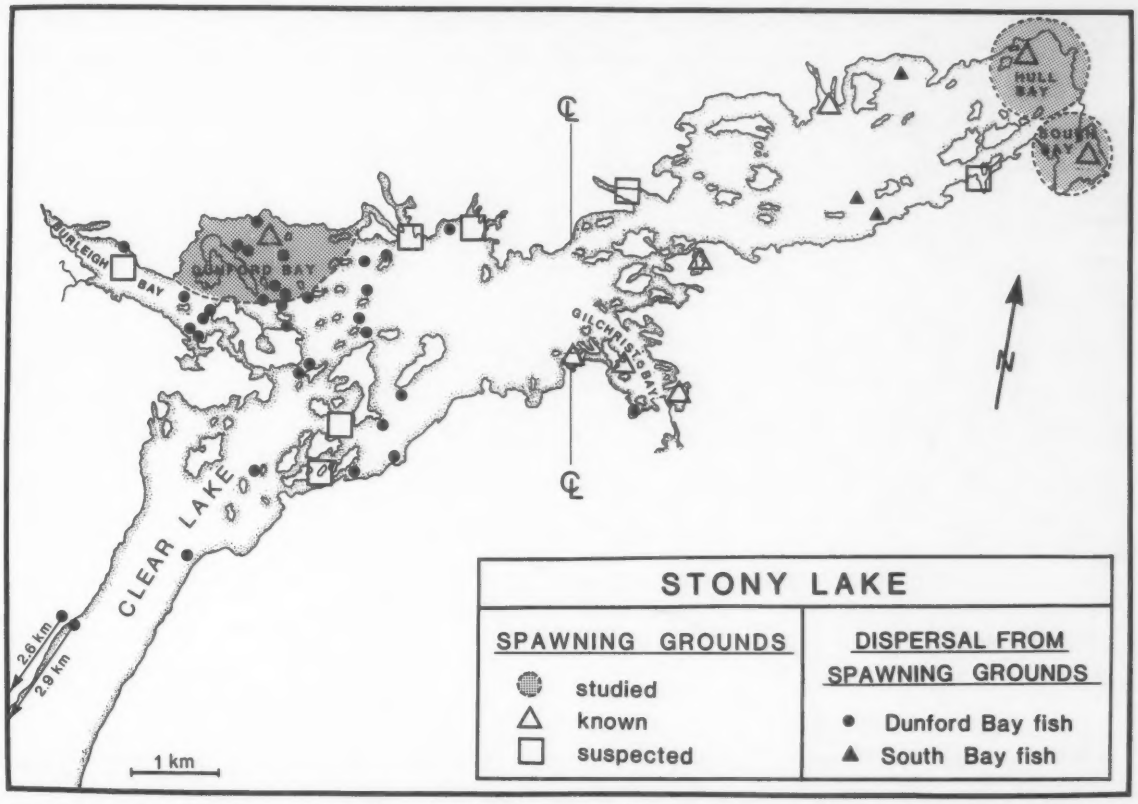

FIG. 3. Stony Lake indicating spawning grounds and location of tagged muskellunge caught by anglers. CL = midpoint of lake, Burleigh Bay to South Bay.

TABLE 1. Muskellunge tagged, released, and recaptured on two spawning grounds of Stony Lake, and marked fish caught by anglers, 1978–86. * = Tagged and released at net site; ** = Includes only first recapture in any year; + Released untagged at net site; NA = not available.

	Dunford Bay (West end)				South and Hulls bays (East end)			
Year	Number nets	new fish	tagged fish recaptured **	tagged fish angled	Number nets	new fish	tagged fish recaptured **	tagged fish angled
1978	9	268*	0	7	0	0	0	0
1979	9	NA	56	5	0	0	0	0
1980	9	196*	15	5	4	11*	0	0
1981	9	152*	31	4	7	40*	3	1
1982	9	781+	52	10	0	0	0	1
1983	9	756+	22	1	0	0	0	1
1984	9	394+	9	1	0	0	0	0
1985	9	288+	12	3	0	0	0	0
1986	9	364+	5	1	0	0	0	0
Totals	81	3199	202	37	11	51	3	3

There was no significant difference (Table 3) between the ages of fish tagged but never recaptured on the spawning ground, and of those recaptured once, nor between ages of those recaptured once and those recaptured two to six times. There was a significant difference between the ages of individuals tagged but never recaptured, and of those recaptured two to six times. Mean age of those recaptured more than once was 6.1 yr whereas that of fish never recaptured was 5.3 yr.

The single age-2 fish was never seen again. Of the remaining 62 new fish three and 4 yr of age, 31 were never seen again, 22 were recaptured on the same spawning ground once, seven were recaptured in two other years, and two were seen three times. The degree of return to net of origin, an adjacent net, or a distant net was similar to that of the older individuals.

Age and length are correlated but length within age-class is extremely variable. The results of comparing fork length with

TABLE 2. History of individual fish with three or more net recaptures in Dunford Bay in separate years. No fish were tagged in 1979. Recaptures were not recorded after 1986.

Tag Number	Sex	Calendar age at tagging	Net of origin	Year of tagging	Recaptures 1st Net	1st Year	2nd Net	2nd Year	3rd Net	3rd Year	4th Net	4th Year	5th Net	5th Year	6th Net	6th Year
05999	F	6	4	1978	4	1979	2	1980	2	1982	2	1983	6	1985	3	1986
06026	F	11	2	1978	2	1979	3	1980	7	1982	2	1985				
06043	F	8	5	1978	4	1979	3	1982	1	1984	7	1986				
06078	M	5	6	1978	5	1979	1	1980	5	1981						
06090	M	7	7	1978	6	1979	7	1980	6	1981						
06116	M	4	6	1978	7	1979	1	1980	9	1981						
06123	M	5	4	1978	3	1979	6	1981	1	1982						
07424	F	7	1	1980	7	1982	2	1983	3	1984	7	1985				
07501	F	11	2	1980	4	1981	3	1982	2	1983						
07853	M	6	7	1981	6	1982	2	1983	1	1985						
07874	M	6	2	1981	2	1982	1	1983	2	1984						
07895	F	6	6	1981	7	1982	5	1983	1	1984	6	1985	3	1986		
07902	F	?	5	1981	2	1982	2	1983	7	1985	3	1986				
07926	M	7	7	1981	7	1982	7	1983	6	1984	7	1986				
07968	F	7	9	1981	5	1982	4	1983	6	1984	3	1985				

TABLE 3. *T*-test of ages and fork lengths of individuals with different histories of return to the Dunford Bay spawning ground. * = significant, *P* greater than 0.01, less than 0.05.

Recaptures	Number	$\bar{x}$	SD	SE	Variances	*T*	df	Prob > *T*
				Age in Years				
None	140	5.3	1.531	0.129	Unequal	−1.797	156.4	0.074
One	88	5.7	1.897	0.202	equal	−1.887	226.0	0.061
None	140	5.3	1.531	0.129	unequal	−2.153	45.9	0.037
2–6	36	6.1	2.019	0.337	equal	−2.531	174.0	0.012*
One	88	5.7	1.897	0.202	unequal	−0.878	61.6	0.383
2–6	36	6.1	2.019	0.337	equal	−0.901	122.0	0.369
				Fork length in mm				
None	476	703.2	122.686	5.623	unequal	−0.243	134.4	0.808
One	100	706.8	136.866	13.687	equal	−0.261	574.0	0.794
None	476	703.2	122.686	5.623	unequal	−1.572	37.0	0.124
2–6	35	746.9	161.027	27.218	equal	−1.987	509.0	0.475*
One	100	706.8	136.866	13.687	unequal	−1.316	52.0	0.194
2–6	35	746.9	161.027	27.218	equal	−1.424	133.0	0.157

TABLE 4. Number of fish recaptured in each net in Dunford Bay 1979–83 on the basis of net of origin (= net at which individual was tagged). The numbers recaptured only in net of origin appear in the left to right diagonal.

Net of origin	Net recaptured 1	2	3	4	5	6	7	8	9
1	**3**	3	1	1	2	0	2	2	4
2	5	**11**	5	4	4	0	3	1	0
3	7	11	**8**	9	3	0	1	2	1
4	1	5	5	**8**	1	2	1	0	3
5	1	2	5	4	**5**	1	1	1	0
6	4	5	1	2	3	**2**	4	1	4
7	1	5	1	0	1	5	**5**	0	0
8	1	4	2	0	0	0	0	**7**	2
9	0	2	1	2	1	1	1	1	**2**

number of times recaptured (Table 3) were similar to those for age. The only significant difference was between individuals never recaptured and those recaptured several times. The mean fork length for fish recaptured several times was approximately 47 mm greater.

Recapture of Marked Fish in Spawning Sites Within Spawning Grounds

Recaptures on a spawning ground suggested that individual fish return not only to a specific ground but to a specific site within that ground (see 05999, 06090, 07501, and 07926 in Table 2). One male (07926) was captured four times at one site (1981, 1982, 1983, and 1986) and once at the nearest site (500 m away) in 1984.

In regard to accuracy of homing to a spawning site within a spawning ground, the ultimate would be for a particular fish to be recaptured in more than 1 yr only in the net of origin. Between 1979 and 1983, for the Dunford Bay spawning ground,

TABLE 5. Number of muskellunge, by net of origin, recaptured at net of origin and at groups of nets 500–1 000 m distant from net of origin. Under 'Number recaptured' the numbers of individuals for increasing areas are accumulative.

Net of origin	Number recaptured				Home : Stray		
	Total all nets	Net of origin	Within 500 m	Within 1 000 m	Same net	Within 500 m	Within 1 000 m
1	18	3	6	7	3:15	6:12	7:11
2	33	11	16	21	11:22	16:17	21:12
3	42	8	17	28	8:34	17:17	28:14
4	26	8	13	18	8:18	13:13	18:8
5	20	5	9	14	5:15	9:11	14:6
6	26	2	6	10	2:24	6:20	10:16
7	18	5	10	11	5:13	10:8	11:7
8	16	7	9	—	7:9	9:7	—
9	11	2	—	2	2:9	—	2:9

TABLE 6. Recapture by areas compared with area of tagging. Areas are arranged from innermost in Dunford Bay (A) to most distant (E). The figure is total number of recaptures in the area, that in brackets is the figure standardized for effort (no. of nets in the area, i.e. A-4, B-1, C-2, D-1, E-1).

Area of tagging	Area of recapture				
	A	B	C	D	E
A	87 (21.8)	10 (10)	9 (4.5)	8 (8)	5 (5)
B	12 (3)	5 (5)	2 (1)	0 (0)	1 (1)
C	19 (4.8)	4 (4)	16 (8)	4 (4)	1 (1)
D	5 (1.3)	1 (1)	2 (1)	2 (2)	1 (1)
E	7 (1.8)	0 (0)	0 (0)	2 (2)	7 (7)
Totals	130 (32.5)	20 (20)	29 (14.5)	16 (16)	15 (15)

a total of 51 muskellunge had a history of recapture only in the net of origin (the left to right diagonal of Table 4). The number of individuals with this history varied from 11 (net 2) to two (nets 6 and 9). Eight such recaptures were recorded at nets 3 and 4, and seven at net 8 (see Fig. 2). However, 155 fish were recaptured in nets other than their net of origin. If recaptures are considered on the basis of proximity to net of origin (Table 5), the ratio of recapture in the area surrounding the net of origin to recapture at greater distance approximates 1:1 at 500 m. When recaptures at nets within 1 000 m of net of origin are accumulated, the ratio is positive for all but three of the nine nets (1, 6, and 9). For four nets (2–5) the positive ratio approaches, or exceeds, 2:1 at 1 000 m.

The general nature of the location of the nine nets in Dunford Bay (= spawning sites) was similar, all sites had characteristics of muskellunge spawning grounds, and spawners were captured at all locations. However, recaptures were highest in the innermost area represented by nets 1–4 (Tables 2 and 4). The data from 1979–83 (Table 4) revealed that recaptures in nets 1–4 (130) were almost twice as high as those in the other five nets (80). To test this result, the recaptures for 1979–83 were grouped according to five areas of the Dunford Bay spawning grounds (Fig. 2) — (A) the innermost area of the main shoreline (nets 1–4), (B) the southwest part of the shore of the horseshoe-shaped island (net 5), (C) the southeast portion of shore of Horseshoe Island (nets 6 and 7), (D) the main shoreline adjacent to A (net 9), and (E) the most remote portion of the main shoreline (net 8).

The number of recaptures in each area was reduced to $\bar{x}$/"area" to compensate for differences in the number of nets in each area (Table 6). As with the simple totals, the figures by area adjusted for effort confirmed that recaptures were highest in A (32.5), next highest in area B (20) and that those in area A were double those in areas C, D, and E.

The recapture figures, standardized for effort (no. fish recaptured ÷ no. nets), were compared on the basis of recaptures by areas against area of origin. Twice as many fish originating in area A were recaptured in area A (21.75), in contrast to being captured in areas B–E. The next highest figure (10) for area A fish was for the adjacent area to the southwest (area B). Recaptures of fish originating in area A were much lower in the remaining areas (C, D, and E). For fish originating in area B, the number of recaptures was slightly higher in B than in A, much lower in areas C, and E, and 0 in area D. Twice as many fish originating in area C were recaptured in C compared to those in A, B, D, and E, there was no clear second best area score, and the number in E was very low. Recaptures of fish originating in area D were the lowest, but virtually twice as many originating there were recaptured there compared to those recaptured in any other one area. The unique points of recaptures of muskellunge originating in area E (farthest from areas A, B, and C) were (1) the low total number, (2) the dominance of fish of area E origin, and (3) none recaptured in areas B or C.

The recapture of fish in the area of origin (e.g. A in A) was compared, as a ratio, to the number recaptured in all other areas (e.g. A in B and C, etc.). The only area with a positive in:out ratio was E (1:0.5). The poorest ratio was for area D (1:2.2). Area A, with the highest number of recaptures, had a ratio of only 1:1.3.

A different area score was derived from the totals (corrected for effort) within areas of only those fish caught in their net of origin (see Table 4 — score for area A = sum of diagonal numbers for nets 1–4 ÷ 4). This yielded similar scores for area A (7.5) and E (7), that for area B (5) was next highest, and those for areas C and D were lowest at 3.5 and 2.

It is important to know whether the somewhat confusing numbers of recaptures in a specific area (A–E) represent a real homing trend, or random return to any area. To test this, those individuals recaptured one or more times in Dunford Bay between 1979 and 1986 were classified into recaptures within area of origin (homing) or recaptures outside of area of origin (random). As stated above, recaptures are the first capture of a tagged fish in any of the years following tagging. In this test, an individual recaptured twice would have been caught in three different years. Data for individuals recaptured several times were used in more than one test (e.g. an individual recaptured twice was used in the tests of second and of first recapture. Three chi-square tests were carried out on those individuals captured once ($N = 135$), twice ($N = 36$), and three times ($N = 14$). The test was of the null hypothesis that choice of area to which an individual returned at spawning time was random. The null hypothesis was rejected in all three cases ($P = < 0.001$, $df = 1$) indicating that muskellunge repeatedly home to a specific area of Dunford Bay at spawning time.

The significant difference in the number of times males and females returned to a specific part of Dunford Bay (areas A–E) was tested. Recaptures of known males and females were used as described above in chi-square tests of the null hypothesis that there is no difference in the frequency with which the two sexes return at spawning time to area of origin. Sample

sizes, and probabilities from chi-square tests (df = 1), for individuals returning one or more times were as follows: once — $N = 75$, $P > 0.05$; twice — $N = 24$, $0.01 < P < 0.05$; and three times — $N = 10$, $P > 0.05$. The null hypothesis that there is no difference in the frequency with which the two sexes return to area of origin could not be rejected.

Thirty muskellunge (19 males, nine females, two unknowns) were captured twice on the Dunford Bay spawning ground in the same season (in, or out of, area of origin) with intervals between captures of 7–16 d.

Location during the Angling Season of Fish Tagged on the Spawning Grounds

In the angling seasons (first Saturday in June to November 15) of the years 1978–86, a total of 40 marked muskellunge were reported by anglers as retained (38), or captured and released (2). Of the 40 reported, 37 had been marked on the Dunford Bay spawning ground, and three on the South Bay spawning ground. The number reported each year (Table 1) varied from a high of 10 in 1982 to one in each of 1984 and 1986. The highest annual number of reports (10) occurred in 1982, the year following that in which the maximum number of marked fish of Dunford Bay origin (616) were at large. The second highest number (7) was in 1978 when a maximum of 286 were at large.

The location of each capture by an angler was plotted (Fig. 3) and, for simplicity, the distance from the spawning ground expressed as falling within a series of concentric circles with centres on the shoreline at the midpoint of the net sites, and with diameters of 1–8 km. The three angled fish of east-end origin were from South Bay (vs. Hull Bay) and were caught in the summer of the year of marking. One was angled 2 km from the spawning ground and two within the 3 km circle.

Not all of the reports of angled fish of Dunford Bay origin had adequate location data. Of the 34 plotted, the numbers caught within various circles were as follows: 1 km — 7, 2 km — 17, 3 km — 6, 4 km — 1, 5 km — 1, 8 km — 1, and outside 8 km — 1. The zone of major dispersal would seem to involve Burleigh Bay to the west of the spawning ground, and the area immediately to the south of the spawning ground (Fig. 3). Two fish were caught as far away as 7.6 and 8.6 km in separately named, but contiguous, Clear Lake. The fish at 5-km distance was caught in Gilchrist Bay (Fig. 3) at the approximate centre of Stony Lake. The narrows near the midpoint of the lake separate all angler recaptures from the two spawning grounds studied. This is parallel to the separation of net recaptures of fish marked and released on those two spawning grounds as described above.

Two marked muskellunge of Dunford Bay origin were angled, released, and recaptured later on the Dunford Bay spawning ground. One female (see 06026, Table 2) of net 2 origin (1978) was caught in net 2 or net 3 during the spawning seasons of 1979 and 1980, and in net 7 in 1982. It was angled and released on June 10, 1984 within the area marked as the Dunford Bay spawning ground in Fig. 3 (summer home range?), and was recaptured in net 2 on the Dunford Bay grounds in the spawning season of 1985. The second individual (06132) originated in net 2 in the 1978 spawning season, was angled and released on August 4, 1978 in Clear Lake, 2.9 km south of the spawning ground, and was recaptured in net 1 of the Dunford Bay spawning ground in the spawning season 4 yr later (1982).

Records of the Ontario Ministry of Natural Resources indicate that angling pressure is fairly evenly distributed over Stony Lake and that the narrow centre section of the lake received as much pressure as other areas.

Discussion

The use of the nets set at Stony Lake as an opportunity to gather information had serious limitations. However, I feel the results provide evidence that muskellunge do carry out directed migration, as defined by Smith (1985), which might be designated reproductive homing. This migration in muskellunge may be consistent with Gerking's (1959) definition (". . .return to a place. . .instead of going to other equally probable places."). It was demonstrated at Nogies Creek that muskellunge with winter home ranges in a small lake by-passed many places deemed suitable by biologists, to seek out a distant "improbable" place (Minor 1981). Further corroboration of choice of less probable locations was provided by the discovery that some muskellunge in Lake Scugog (Fig. 1), rather than moving to the major known spawning area at the south end of the lake moved north in the outlet river bypassing "more suitable places," to move up tiny Mariposa Brook to a distant, headwater marsh. Young-of-the-year and spawned-out adults were found 10 km from the lake. The Mariposa marsh was shallow and brushy, much like the upstream site chosen by lake-dwelling fish at Nogies Creek.

Distance travelled by muskellunge to and from spawning grounds in these migrations would appear to be positively correlated with lake area or available stream distance. Records for Nogies Creek, Lake Scugog, Stony Lake, and the St. Lawrence River support this. The present known maximum for individual muskellunge would appear to be a round trip of 156 km, and a one-way trip of 98 km, in the St. Lawrence River (S. LePan, NYDEC, Watertown, NY, pers. comm.).

It seems obvious from the work at Stony Lake that muskellunge do home to particular spawning grounds. Net recaptures and angler reports strongly suggest there are at least two discrete spawning populations using separate spawning grounds. For at least those spawners using the two grounds studied, which are at maximum separation (12.8 lake km), it would appear there is not only reproductive isolation but also isolation in summer. No information is available on interchange between less-separated pairs of grounds (Fig. 3). The area at the centre of the lake has one of the heaviest densities of islands and lowest area of water greater than 2 m in depth. In contrast the "thoroughfare" to Clear Lake, although studded with islands, has considerable water over 5 m in depth. It is possible that the isolation between muskellunge in the east and west parts of Stony Lake represents the joining of two previously separate bodies of water.

Considering the low density of most muskellunge populations, the number of spawners appearing annually on one (Dunford Bay) of possibly many grounds in one lake, seemed moderately high (183–833 per year).

One of the most significant discoveries was the degree to which a small number of individual muskellunge repeatedly homed to a spawning ground. One individual (05999 Table 2) was captured a total of seven times (6 recaptures). Failure to capture that fish on that ground in 1981 and 1984 does not mean it was not there. The return rate over the whole period 1979–86 was 32.8% of fish marked, and 20.9% after 1 yr. These figures, and the fact that both sexes were involved, at least

suggests that individuals spawn every year and repeatedly home to a particular spawning ground.

A surprise was the number of new fish appearing on the Dunford ground each year. New fish constituted 83 to 98% of the number of fish handled annually. Conversely fish homing to the ground ranged from 16.9% (1981) to 1.4% (1986). The low numbers of new fish in the years 1979–81, may indicate that the research crew did not see all the new fish taken by the nets in those years, as indicated above. The size and age of new fish appearing on the grounds suggests the large number resulted from annual recruitment into the ranks of those first attaining sexual maturity. One other possible explanation is that some new fish of spawning age do stray from one spawning ground to nearby spawning grounds in different years. Another is that Dunford Bay is only part of a larger spawning ground involving Burleigh Bay to the west and two other locations to the east (Fig. 3). There was some consideration that younger, smaller individuals arriving on a spawning ground for the first time might stray to a greater extent than individuals which had found their way back there one or more times. The data are not highly suited to the test as it was impossible to tell in 1978 whether any of those arriving on the Dunford Bay spawning ground were arriving there for the first time. The data available did not reveal any considerable relationship between size or age and the tendency to return or stray. There was only slight difference in age and size between those individuals which were never seen again on a spawning ground, and those for individuals which returned several times (Table 3).

It is usually assumed that in Ontario a significant number of male muskellunge first attain sexual maturity at ages 4–6 and females at 5–7 yr. At Stony Lake a surprisingly high number of new fish were between two and 4 yr of age, and the single age-2 fish was a female. Of those individuals three and 4 yr of age, 90% were male. It is not known, however, the degree to which these unusually young fish participated in spawning. The only explanation I can provide for the discrepency in number of very young new fish seen in the three capture years (56 in 1978, three in 1980, four in 1981) is the possibility of highly successful year classes in 1974 and 1975.

Within spawning grounds, individual fish appear to select and return to particular areas. The inner shoreline portion of the Dunford Bay ground (nets 1–4, Fig. 3) was the most heavily used and homed to. There was moderate evidence of repeated homing to a very restricted single spawning site (one net) within Dunford Bay. There is better evidence of return to a spawning site when sites within 1 000 m are combined (Tables 4 and 5). When sites (net locations) were grouped into areas (A–E of Table 6) it can be shown there is statistically sound evidence of homing to a particular area as opposed to random movement to any area. In addition, males and females home to an area with equal frequency.

There were 30 individuals recaptured twice in a single season. The interval between recaptures ranged from 1–20 d. Those with shorter intervals may constitute the wandering of fish with less adaptation than others to a specific spawning site or area. Those with the longer interval may represent examples of the multiple spawning in muskellunge described by Lebeau (1983).

This Stony Lake work provides no direct evidence that repeat spawners are returning to their natal spawning ground, although that may be the case.

Angler records of marked fish (Fig. 3) indicated the spawners using sites within Dunford Bay spawning grounds probably had summer home ranges as close as Dunford Bay and as far away as 8.6 km in contiguous Clear Lake. No fish went east beyond the narrows near the midpoint of the lake. No fish using the South Bay grounds moved west of the midpoint. Choice of spawning ground, and of summer home range may also reflect the possibility that Stony Lake represents two previously separate bodies of water. That muskellunge on these summer home ranges home to a specific spawning ground is also indicated from the capture of individuals on that ground in spawning seasons before and after it was located elsewhere on a summer home range.

Pathways (Tesch 1979), guidance mechanisms and environmental cues (Smith 1985, McKeown 1984), and learning a route (Dodson 1988) have long been debated in regard to their role in homing in fishes. Richard (1979) suggested pike home to spawning grounds by recognizing the smell of the characteristic decayed organic material. Tesch (1979) devised a classification of orientation which included one referred to as "Shoreline Orientation." The general shallow water affinity of the muskellunge would make it a likely candidate for this latter concept. However, the location of the nets, and their catches of new and recaptured muskellunge, would suggest strongly that fish approaching the Dunford Bay spawning ground, and to a large extent terminating in the area of nets 1–4 (Fig. 2), moved in from the south through the centre of Dunford Bay, not along the north shore of the lake.

It would appear that the spawning and nursery phases of the life history of muskellunge are unusually critical in regard to population strength. Factors determining choice of one spawning ground or site seem complex (Dombeck 1979). Sites distant from winter or summer home range are often chosen over closer sites deemed (by humans) to be equally suitable. If obligatory homing to a limited number of such sites is a reality, then muskellunge populations are extremely vulnerable to the sort of habitat changes almost universally associated with the development of shorelines and areas of shallow water for human use. Smith (1985) spoke of the increased vulnerability of obligatory journeys to human interference but Leider (1989) suggested that when the natal streams of migratory steelhead trout, *Oncorhynchus mykiss*, were obstructed, migrating adults bypassed them and reproduced in tributaries further up river.

If the assumptions made here about reproductive homing and summer dispersal are correct, it may be necessary to manage muskellunge in a lake on the basis of more than one discrete population. In addition, the adaptive advantage to a population of reproductive homing to a highly suitable spawning ground could be diluted or lost by continual additions of hatchery stock derived from wild spawners from a different population (Smith 1985).

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Measuring Epilithic Bacterial Production In Streams

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Techniques are presented for the measurement of bacterial production (by the rate of ^{3}H-TdR incorporation into DNA), isotope dilution, time course of incorporation of nucleoside, and disturbance artifacts in natural epilithic (on rock) communities of headwater streams. The epilithon in riffles was subsampled by carefully chipping upper rock surfaces. Chips were placed in test tubes and incubated in situ. Test tubes were rotated to reduce the formation of artificial diffusion barriers to TdR transport. DNA was isolated using a double filtration technique. Summertime production had a range of 1.3–51 mg $C \cdot m^{-2} \cdot h^{-1}$ in five southern Ontario streams. Precursors to DNA synthesis, which diluted ^{3}H-TdR, had a range of 63–440 nM. Incorporation of ^{3}H-TdR was linear for at least 1 h. Disturbance artifacts did not appear from rock chipping or from extended sample rotation. The techniques can be applied to other microbial groups from various aquatic hard substrata.

Des techniques permettant de mesurer la production de bactéries (d'après le taux d'incorporation de la ^{3}H-TdR dans l'ADN), la dilution d'un isotope, le temps d'incorporation d'un nucléoside et les erreurs expérimentales dues aux artéfacts dans des communautés épilithiques (vivant sur la roche) naturelles de cours d'eau d'amont sont présentées. La partie supérieure de roches se trouvant en eaux vives a été soigneusement grattée de façon à obtenir des échantillons de communauté épilithique. Les fragments de roche ont été déposés dans des éprouvettes et incubés in situ. Les éprouvettes ont été agitées de façon à limiter la formation de barrières artificielles à la diffusion de la TdR. L'ADN a été isolé au moyen d'une technique de filtration double. La production estivale variait entre 1,3 et 51 mg $C \cdot m^{-2} \cdot h^{-1}$ dans cinq cours d'eau du sud de l'Ontario. La concentration des précurseurs de la synthèse de l'ADN, qui diluaient la ^{3}H-TdR, variait entre 63 et 440 nM. Durant au moins une heure, l'incorporation de la ^{3}H-TdR était linéaire. La technique de prélèvement des fragments rocheux et l'agitation prolongée des échantillons ne semblent pas avoir faussées les résultats. Ces techniques peuvent être appliquées à d'autres groupes microbiens vivant sur divers substrats aquatiques durs.

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Despite the acknowledged importance of microorganisms to bioenergetic processes in stream ecology, the measurement of lotic microbial production is in its infancy (Benke et al. 1988). Recently, techniques have been developed for the measurement of heterotrophic bacterial production in riverine sediment and water column habitats (e.g. Findlay et al. 1984). However, a comprehensive technique for measuring heterotrophic bacterial productivity in the epilithon is still lacking.

Estimates of bacterial productivity in the epilithon on artificial substrata in streams have recently been made (e.g. Kaplan and Bott 1989), but there are disadvantages in the use of artificial substrata in analyzing aquatic benthic communities (e.g. Rosenberg and Resh 1982; Morin, 1987; McGuinness 1989). For example, stream riffles are physically heterogenous environments, and artificial substrata may not adequately duplicate this variability. Furthermore, considerable effort must be expended to confirm if and when an artificial substratum has a community that is similar in structure and function to that of the surrounding microbial communities.

Because of the limitations of existing methods and the lack of information on epilithic bacterial productivity a method was developed for measuring heterotrophic bacterial production directly on rock surfaces. Additional experiments were also designed and conducted to correct for isotope dilution and check for linear incorporation of tritiated thymidine and disturbance artifacts. This research was part of a broader study which examined bacterial, algal, and invertebrate communities in southern Ontario streams.

Materials and Methods

Experiments were conducted twice on one riffle in each of five southern Ontario streams (stream order ranged from 2 to 3). Limestone Creek (LC), Hanlon Creek (HC), and a tributary to the West Credit River (WC) had forested watersheds, while Swan Creek (SC) and Carol Creek (CC) were open streams bordered by meadows. All riffles had an underlying cobble substratum.

All incubations were conducted with 1.48 MBq of [methyl-^{3}H]TdR (final conc. 60–84 nM) which was supplied by either ICN (2.2–2.5 TBq·mmol^{-1}, Cat # 24039 or 24060) or NEN (3.1 TBq·mmol^{-1}, Cat # NET 027Z).

Time Course of Incorporation of ^{3}H-TdR

A time course experiment was conducted at site SC to determine if incorporation of ^{3}H-TdR into cellular DNA was linear

over extended incubation periods. Site SC was assumed the most probable to experience substrate limitation because maximal incorporation rates were observed here.

A rock with an epilithon (upper side) which appeared homogeneously distributed and representative of other rocks in the riffle was selected. The rock was carefully broken into chips (1–3 cm^2) with a chisel and hammer. All chipping was conducted in a manner that minimized disturbance to the epilithon (see below). The area of the epilithon on each rock chip was traced onto clear plastic, and later converted gravimetrically to area. Then each chip was randomly placed in a test tube (18 × 64 mm) which contained 8 mL of stream water. Test tubes were organized in a rack in six time treatments (one killed control and two live samples per treatment). They were simultaneously injected with ^{3}H-TdR (60 nM, final conc.), capped, and submerged in a bin containing stream water at ambient temperature. In the bin, samples were incubated for either 5, 10, 20, 30, 45, or 60 min, depending on treatment. The rack of samples was continuously rotated at 15 rpm to reduce the formation of artificial diffusion barriers to thymidine transport during the incubation.

Incubations were stopped with 0.6 N NaOH, 0.1% SDS, and 25 mM EDTA (final conc.). Samples were then put on ice, transported to the laboratory, and stored at 5°C for 18–24 h before being processed. Before rock chipping commenced, samples of epilithon were scraped from each rock used; these were later analyzed for ash free dry weight (AFDW) which was determined from the difference between the dry weight (55°C, 24 h) and the ash weight (500°C, 2 h) of the samples.

In the laboratory, samples were placed in a water bath (95°C for 1 h) to complete cell lysis and RNA hydrolysis. Rock chips were then removed and the remaining solution containing the labelled macromolecules was cooled to 0°C and neutralized with HC1. The DNA and protein were precipitated by acidification with cold (0°C) TCA (5% wt/vol final conc.). Approximately, 0.25 g of celite (Fisher Scientific) was added to each acidified sample 10 min after acidification. Samples were shaken to resuspend the celite and then decanted onto Sartorius nitrocellulose membrane filters (47 mm, 0.2 μm pore size) which were previously wetted with unlabelled thymidine (10 μM) and supported on Nalgene polysulfone filterware. Samples were filtered (35 KPa vacuum pressure) simultaneously on a 29 unit filter rack. Celite was essential in assisting the passage of these often highly organic samples through the nitrocellulose filters. Towers and filters were rinsed and "ringed" with cold 5% TCA to remove unincorporated ^{3}H-TdR.

Filters and precipitate were carefully removed and inserted into test tubes which were then filled with TCA (10% wt/vol). Test tubes were placed in a water bath at 95°C for a half hour to hydrolyse DNA. Samples were removed, cooled, and then refiltered, as above. The filtrate with the hydrolysed DNA was collected, and assayed for radioactivity in DNA. Samples, in 10 mL of ACS II fluor (Amersham Corp.), were counted in a LKB-Wallac Rackbeta (model 1217) liquid scintillation counter. Quenching was corrected by the external standard channels ratio method. DPM in DNA were corrected for control and background counts and recovery efficiency of cellular DNA (see below). The above laboratory procedure was also useful for processing highly organic sediment samples (6–59% AFDW) from the same streams (unpubl. data).

Approximately, 6.5 h were required to process 28 samples in the laboratory with the technique. This included the time from the start of the alkaline hot water bath treatment to the adding of scintillation fluor. Modifications of the technique used by Wicks and Robarts (1987) were attempted (to further reduce sampling handling time), but were found to be inappropriate: lower recoveries of ^{3}H-DNA were obtained (44.5 ± 12%, $n = 5$), samples often clogged the filters, and only a limited number of samples could be filtered at once in a fume hood. The technique was even more problematic with sediment samples from these streams (unpubl. data).

Recovery Efficiency of Bacterial DNA

Tritiated DNA [thymine-Me-^{3}H] from *Escherichia coli* (New England Nuclear, 440 MBq·mg^{-1}, cat. # NET-561) was used to estimate recovery of bacterial DNA. This stock was diluted into a working solution which consisted of 25 μg of DNA from salmon testes (Sigma Chemical Co. cat # D-1626), 0.232 MBq of stock DNA in 5 mL of 10 mM Tris buffer and 10 mM EDTA at pH 7.0 (procedure modified from Findlay et al. 1984). Two chips from the rock used for the isotope dilution experiment were added to two test tubes containing 8 mL of stream water. These samples were killed (as described above), injected with the ^{3}H-DNA working solution, capped and then placed beside the production and isotope dilution test tubes in the rack in the rotating bin. Recovery efficiency was also determined for the time course and disturbance artifact experiments in a similar manner. The area of the epilithon on these chips was recorded as described above.

Aliquots of the ^{3}H-DNA working solution were radioassayed to determine the activity of the ^{3}H-DNA added to samples in the field. The radioassay consisted of hydrolysing the aliquot of ^{3}H-DNA in 1 mL of 10% (w/v) TCA at 95°C for 1 h. The activity in the aliquot was counted as described above.

Recovery samples were processed in the laboratory as described for time course samples. After the second filtration step, the nitrocellulose filters of the recovery samples were set aside for future determination of the activity of ^{3}H-DNA that may have remained on them, due to incomplete DNA hydrolysis (e.g. see Servais et al. 1987). These filters were suspended in 0.04 N NaOH and placed in a hot water bath (95°C) for 1 h to elute the DNA into solution. These solutions were neutralized and then radioassayed for DPM in DNA.

Isotope Dilution

The degree of dilution of ^{3}H-TdR from cellular and extracellular sources (i.e. thymine, thymidine, dTMP, dTDP, and dTTP) can vary spatially and temporally and often has the greatest influence on the calculation of production (Findlay et al. 1984; Moriarty 1986; Chrzanowski, 1988). Four rocks were chosen from each riffle with a stratified random sampling design. A sample of the epilithon was chipped off from each rock and used in the production experiment (see below). The largest rock which appeared (visually) intermediate in characteristics (e.g. in thickness and composition of the epilithon) between the four rocks selected, was further broken up into chips for an isotope dilution experiment. Occasionally, none of these four rocks was suitable for this experiment, e.g. they were not large enough to supply the required number of chips. In this case, a large representative rock was non-randomly selected from the riffle and chipped into samples for the isotope dilution experiment.

The specific activity of ^{3}H-TTP, the precursor to DNA, was determined for each production experiment by the isotope dilution method (Pollard and Moriarty 1984). The isotope dilution

series consisted of five treatments (20 test tubes total: one killed control and three live samples per treatment) of non-radioactive thymidine (range 0–1187 nM) (Sigma Chemical Co., Cat. # T-5018). The isotope dilution samples were incubated alongside the production samples. The epilithic area on each rock chip was determined as described above. Samples were stored, processed, and corrected as for the time course experiment samples.

Checks on Methodology

The epilithic area on control chips of four production and isotope dilution series experiments was recorded. This was later used to confirm that the radioactivity on control chips was not a function of the epilithic area on these chips.

Steps in the methodology may have introduced significant disturbances, e.g. through chipping or extended rotation of samples. Therefore, a method was developed to test directly for disturbance artifacts in isotope dilution and production experiments.

To test if an artifact was introduced with extended rotation of samples, a rock with an epilithon which appeared homogeneously distributed and representative of the epilithon on other rocks in the riffle was selected at site SC. The rock was broken into chips which were randomly assigned to five treatments (one killed control and two live samples per treatment). All samples commenced rotating simultaneously in the bin, but the injection of ^{3}H-TdR (1.48 MBq) was staggered over time between treatments; all treatments were incubated for 15 min. For example, treatment one was injected at the start of rotation and stopped 15 min later; treatment two was injected after it had been rotating for 17 min and was rotated for a further 15 min before it was stopped; treatment three was injected after it had been rotating for 70 min and was rotated for a further 15 min before it was stopped, and so forth for the remaining treatments. Samples were stopped, stored, processed, and corrected as in the time course experiment.

A considerable disturbance may be created from chipping a rock surface, e.g., part of the epilithon may be lost or altered with continued pounding. A number of precautions were taken to reduce such disturbances. Rocks were removed carefully from the riffle to limit loss of loose detritus. Rocks were submerged in a calm section of stream to dampen the effects of pounding. In addition, they were placed on a solid substratum, e.g., bedrock, and were struck along points of weakness, e.g., fissures, to hasten splitting.

Rocks designated for the isotope dilution experiment were initially fractured into two or more large sections. Chips were then removed from these sections, so that the effects of pounding were not all concentrated on one rock. We have noticed a decrease in incorporation of nucleoside when pounding is excessive and limited to only one rock section (unpubl. data). Therefore, we recommend this initial fracturing, before chips are removed for experiments. A large chisel (2.5 cm wide tip) was used to initially split the rock into large sections, while a smaller chisel (1 cm wide) was used to split the sections into chips. As rock chips were produced, they were added sequentially across treatments of the isotope dilution series; this distributed any cumulative bias among treatments.

Although these precautions were taken, an experiment was conducted to determine the effect of continuous pounding on rock sections. At site SC, a representative rock with a homogeneous epilithon was selected and broken in half. Each half was pounded to successively remove rock chips. The total number of pounds delivered to each rock section was noted with the removal of each rock chip. Thus, the rate of incorporation of ^{3}H-TdR could be examined as a function of the number of pounds delivered to a rock section.

Ten chips were removed (five from each half) and simultaneously incubated for 20 min. Every two live samples were accompanied by a killed control sample. Samples were stopped, stored, processed, and corrected as described for the time course experiment.

Cellular Biovolume and Abundance

On each site visit, a sample of epilithon was scraped off each of the four experimental rocks and preserved in 5% formalin (vol/vol) at 5°C. Counting of bacteria was completed (within 5 wk after collection) by the direct count technique (Hobbie et al. 1977). Each sample was diluted and homogenized for 5 min in a Waring blender. A subsample of the homogenate was stained with DAPI (final conc. 1 $\mu g \cdot mL^{-1}$) (Porter and Feig 1980; Coleman 1980) for 10 min and then filtered. Cell abundance was determined by counting the bacteria in ten randomly selected fields per slide (1250 × power) and was standardized by epilithic area (m^2). Biovolume was determined from 50 randomly selected cells per slide. Volumes of cocci were calculated as spheres, and rods were assumed to be cylinders. The average cell volume was the weighted average of the volume of coccus and rod-shaped bacteria. Overall, there were four replicates (one from each rock) of cell biomass and abundance for each site visit.

Production

A sample of the epilithon was chipped from each of the four selected rocks. Areas of epilithon were recorded as described above. Samples were incubated from 20 to 90 min, depending on stream temperature. A control chip was included with the production samples; this was stopped before live samples received ^{3}H-TdR. Samples were stopped, stored, processed, and corrected as for the time course experiment. In addition, production samples were corrected for isotope dilution.

Production (measured in mg $C \cdot m^{-2} \cdot h^{-1}$) on each of the four chips was calculated from the following formula (modified from Findlay et al. 1984):

$$P = (\text{DPM in DNA/S.A.})\ (\text{Cells/TdR})\ (\text{C/cell})\ (1000\ mg \cdot g^{-1})\ (10\ 000\ cm^2 \cdot m^{-2}).$$

Where DPM in DNA = DPM incorporated into $DNA \cdot cm^{-2} \cdot h^{-1}$, SA (specific activity) = DPM of ^{3}H-TdR added per effective pool concentration (determined from isotope dilution series), Cells/TdR = cells produced per mole of TdR incorporated (2×10^{18} cells produced per mole of TdR incorporated, Moriarty 1986), C/cell = average C content per cell, estimated from the product of the mean cellular biovolume on each rock chip, and the amount of $C \cdot \mu m^{-3}$ of cell volume. After reviewing the literature, a planktonic value of 1.2×10^{-13} g $C \cdot \mu m^{-3}$ derived from Watson et al. (1977) was applied (see Bell and Ahlgren (1987) for a brief discussion). The two factors, 1000 $mg \cdot g^{-1}$ and 10 000 $cm^2 \cdot m^{-2}$ convert production from grams of carbon per cm^2 to mg carbon per m^2. Four replicate estimates of production were obtained on each site visit from the four chips which were removed from the four rocks selected from the riffle. Data are presented as $\bar{x} \pm$ 95% C.I. (n) unless stated otherwise.

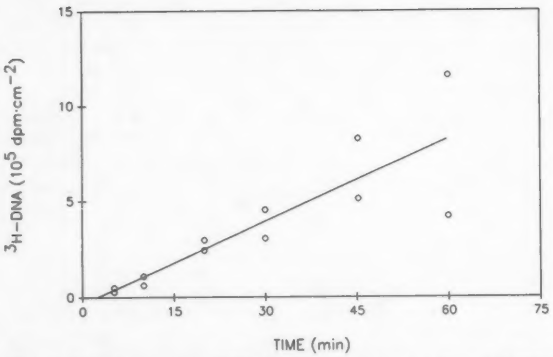

FIG. 1. The time course of ^{3}H-TdR incorporation into bacterial DNA at site SC on August 31, 1988 ($R^2=0.73$, $n=12$). The *Y* axis is DPM in bacterial DNA per cm^2. The *X* axis is the length of time a sample was incubated with ^{3}H-TdR (1.48 MBq per sample, 60 nM final conc.).

Results and Discussion

Time Course of Incorporation of ^{3}H-TdR

Although there is heteroscedasticity in the data (Fig. 1), the time course of ^{3}H-TdR incorporation (1.48 MBq, 60 nM final conc.) into bacterial DNA appears to be linear ($R^2=0.73$, $n=12$) for at least 60 min at 24°C on rock chips from a rock which had a mean AFDW of 23 ± 17 mg·cm^{-2} ($n=4$). Samples of production and isotope dilution experiments were incubated for up to 90 min at the forested sites HC and LC. These experiments were conducted at low temperatures (15.3 and 16°C, respectively), where the rate of incorporation of ^{3}H-TdR was minimal. These bacterial communities probably did not experience substrate limitation, i.e. after 1 h of incubation.

Recovery Efficiency of Bacterial DNA

A mean of 58 ± 11% ($n=10$) of the added ^{3}H-DNA was extracted from the recovery samples. The recovery of ^{3}H-DNA was variable between sites and at the same site between sampling dates (Table 1). Recovery was often lower than reported for sediment studies (e.g. Findlay et al. 1984) and water column studies (e.g. Wicks and Robarts 1987). Different sediment types have been reported to give different efficiencies of DNA recovery with similar extraction procedures (e.g. see Bell and Ahlgren 1987). The technique was not optimized for extraction of DNA when environmental conditions changed between streams. This might account for the lower and more variable recovery.

The efficiency of recovery of ^{3}H-DNA increased as the epilithic surface area increases ($R^2=0.52$, $P<0.05$, and $n=10$) on the recovery rock chips (Fig. 2). The increased surface area of the rock chips may have retarded the degradation of labelled DNA. Until the cause of this relationship is clarified, chips used in recovery experiments should be similar in epilithic area to those used in the production experiment, otherwise estimates of recovery of DNA from production samples may be biased.

The efficiency of recovery of added ^{3}H-DNA did not appear related ($R^2=0.026$, $P>0.05$, and $n=10$) to the AFDW. The lack of relationship may stem from the method used to measure AFDW: it was measured from a separate section of the same rock, but not from the recovery chips themselves. Because the AFDW on a single rock can be quite heterogeneous (e.g. 23 ± 17 mg·cm^{-2}, $n=4$), it is possible that samples for recovery efficiency and AFDW were aliased.

Radioanalysis of filters used to process recovery samples revealed that only 12 ± 3.9% ($n=10$) of the added ^{3}H-DNA remained on the second nitrocellulose filter. This is an improvement of the results reported by Servais et al. (1987) who found that 45% of *E. coli* DNA (treated in 5% TCA at 100°C for 2 h) did not undergo hydrolysis.

Isotope Dilution

The majority of the isotope dilution plots (7 of 10) have coefficients of determination (R^2) that are either equal to or greater than 0.50 (Table 1). In view of the heterogeneous distribution of the AFDW on many rocks, these high coefficients of determination were encouraging. Typical examples of isotope dilution plots are illustrated in Fig. 3.

Coefficients of determination in isotope dilution plots were higher for open sites (Table 1), where temperatures were elevated (see below for temperatures) and the incorporation of ^{3}H-TdR into DNA was greater. Incorporation was insufficient at site LC (June 28) and a poor linear fit (i.e. $R^2=0.16$) resulted. In warmer waters in August, a better estimate of the effective pool concentration diluting the added ^{3}H-TdR was obtained for this site.

TABLE 1. Bacterial production and associated variables in the epilithon at each field site from June to August, 1988.

Site (canopy type)	Sampling date	Recovery efficiency (%)[a]	Effective pool concentration (nanomoles)[b]	Mean bacterial production (mg C·m^{-2}·h^{-1})[c]	Mean bacterial doubling time (*h*)[cd]
Hanlon Cr.	June 21	75 – 77	85 (0.66)	2.5 ± 1.7	20 ± 19
(forested)	July 19	34 – 37	93 (0.67)	2.6 ± 1.6	18 ± 23
Limestone Cr.	June 28	39 – 42	440 (0.16)	4.6 ± 3.9	27 ± 7.9
(forested)	August 2	33 – 60	107 (0.64)	1.3 ± 1.2	105 ± 171
West Credit R.	July 12	63 – 68	63 (0.37)	3.0 ± 6.9	49 ± 115
(forested)	July 28	51 – 61	179 (0.44)	3.2 ± 4.1	15 ± 13
Carol Cr.	June 3	57 – 75	209 (0.50)	37 ± 70	7.6 ± 7.4
(open)	July 15	73 – 74	196 (0.87)	15 ± 24	4.1 ± 4.0
Swan Cr.	June 30	35 – 58	267 (0.60)	8.2 ± 6.3	11 ± 8.9
(open)	August 4	76 – 78	272 (0.78)	51 ± 52	2.0 ± 1.8

[a]Range in recovery efficiency of DNA based on two replicates per sampling date
[b]From isotope dilution plots. Coefficient of determination (R^2) is in brackets.
[c]Mean and 95% C.I. Means are based on four replicates per sampling date.
[d]Equal to bacterial biomass (mg C·m^{-2}) divided by bacterial production (mg C·m^{-2}·h^{-1}).

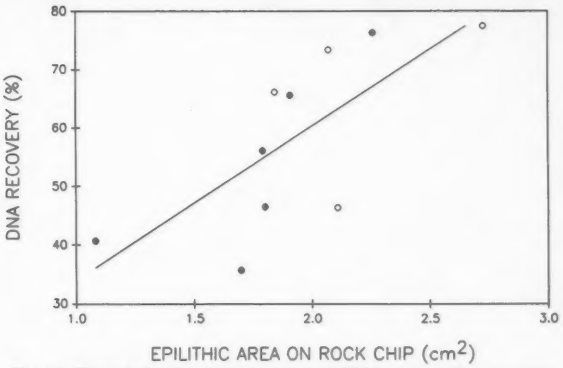

FIG. 2. The relationship between mean epilithic area and mean recovery of ^{3}H-DNA of recovery samples ($n=2$) on each sampling date ($P<0.05$, and $n=10$). Forested (•) and open (○) measurements.

Although production was determined in the epilithon of four randomly chosen rocks, the degree of isotope dilution was calculated from only one of these rocks (the rock which appeared to have characteristics intermediate to the others). The degree of isotope dilution of this rock was applied to the remaining rocks to calculate their production. Productivity estimates for each of these rocks may have been more accurate if an isotope dilution series had been performed on each. However, this was beyond the scope of this research. Although production at each site may be more variable than reported, the estimate of the mean rate should be unbiased.

Conducting time-consuming isotope dilution series may be avoidable if sufficiently high concentrations of thymidine are added to inhibit de novo synthesis of dTMP (See Pollard and Moriarty (1984) and Bell (1986). However, a high specific activity of ^{3}H-TdR should be used for inhibition when incorporation rates are low (e.g. at cold forested sites), otherwise there will be inadequate separation in radioactivity between controls and live samples.

The effective pool concentrations were substantial and fluctuated between sites and at the same site on different dates (Table 1). Therefore, unless de novo synthesis of dTMP can be inhibited, isotope dilution should be measured when spatial and temporal scales change between experiments. The effective pool concentrations in the epilithon (Table 1) fell between those determined in parallel studies of the water column (15–65 nM) and sediment (226–7103 nM) habitats in these streams (unpubl. data).

The isotope dilution technique can be improved. Increased replication in the series, e.g. in replicates or treatments, or both, would improve the precision of measuring isotope dilution. Larger samples of the epilithon could be used in each replicate to increase total incorporation, especially at sites like LC, where incorporation was often very low. An increase in the epilithic area of samples may also increase recovery efficiency of bacterial DNA (see Fig. 2 and related text).

Checks on Methodology

In production experiments, radioactivity of controls (corrected for sample dilution in the laboratory) was 1.2–19% of that of live samples (corrected for sample dilution and recovery efficiency). Radioactivity of control chips from four isotope dilution and production experiments appears to be independent of epilithic area (Fig. 4). Although a bias does not seem to be present, these results should not be extrapolated to other hard substrata without similar tests being conducted.

The technique of measuring bacterial production via the rate of incorporation of ^{3}H-TdR into DNA is less subject to disturbance artifacts due to the conservative nature of DNA (Moriarty et al. 1985; Dobbs et al. 1989). However, Moriarty and Pollard (1981) indirectly detected a disturbance artifact while using the technique. A disturbance artifact may have been introduced into our experiments as the samples incubated in the field bin. However, the rate of incorporation of ^{3}H-TdR during 15 min incubation periods did not significantly change ($R^2=0.038$, $P>0.05$, and $n=10$) over a 67 min rotating period; the experiment was conducted at 21°C on chips from a rock with a mean AFDW of 31.3 ± 33.9 mg C·cm^{-2} ($n=3$). The production and isotope dilution experiments were thus probably free of a significant time disturbance artifact.

Samples were rotated during incubation to reduce the formation of artificial diffusion barriers to thymidine transport into the epilithon. A variety of organisms are affected by water current (Whitford and Schumacher 1964; Horner and Welch 1981; Cahoon 1988). We assumed that estimates of productivity would be more accurate if the samples were exposed to a flow of water. However, the influence of the rate of rotation of the samples on the rate of incorporation of nucleoside warrants further investigation.

Rock splitting and chipping is a procedure likely to introduce a disturbance artifact. However, an artifact was not detected ($R^2=0.002$, $P>0.05$, and $n=10$) at 21°C with chips from a rock which had a mean AFDW of 13 ± 2.6 mg C·cm^{-2} ($n=4$). Nor was there evidence of a time related disturbance artifact ($R^2=0.010$, $P>0.05$, and $n=10$) during this pounding experiment. Experiments that detect and measure disturbance artifacts, such as those developed here, can be incorporated into future studies to increase confidence in the accuracy of bacterial productivity estimates.

Cellular Biovolume and Abundance

Mean bacterial cell volume at each site had a range of 0.15–0.32 μm^3. The mean volume for all sites was 0.25 ± 0.044 μm^3 ($n=10$). Mean bacterial abundance at forested sites was ($2.5 \times 10^{12} \pm 1.3 \times 10^{12}$ cells·m^{-2}, $n=6$), which is very similar to the mean bacterial abundance found at open sites ($2.9 \times 10^{12} \pm 2.0 \times 10^{12}$ cells·m^{-2}, $n=4$). Mean bacterial biomass at each site had a range of 35–145 mg C·m^{-2} and was similar between forested and open sites.

Heterotrophic Bacterial Production

Production and isotope dilution experiments were conducted at ambient water column temperatures between 13 and 21°C at forested sites and between 20 and 30°C at open sites. The mean AFDW on rocks chosen for production experiments was 9.9 ± 7.1 mg C·cm^{-2} ($n=6$) at forested sites and 11.8 ± 7.0 mg C·cm^{-2} ($n=4$) at open sites.

Mean production at forested sites was 2.9 ± 1.1 mg C·m^{-2}·h^{-1} ($n=6$) while at open sites it was 28 ± 32 mg C·m^{-2}·h^{-1} ($n=4$) (Table 1). The variability of production at each site (Table 1) was probably related to the heterogeneous distribution of the epilithon in riffles. For example, the mean coefficient of variation for the AFDW at each site was 56%.

These were probably maximal rates of production since the experiments were conducted during peak daytime temperatures

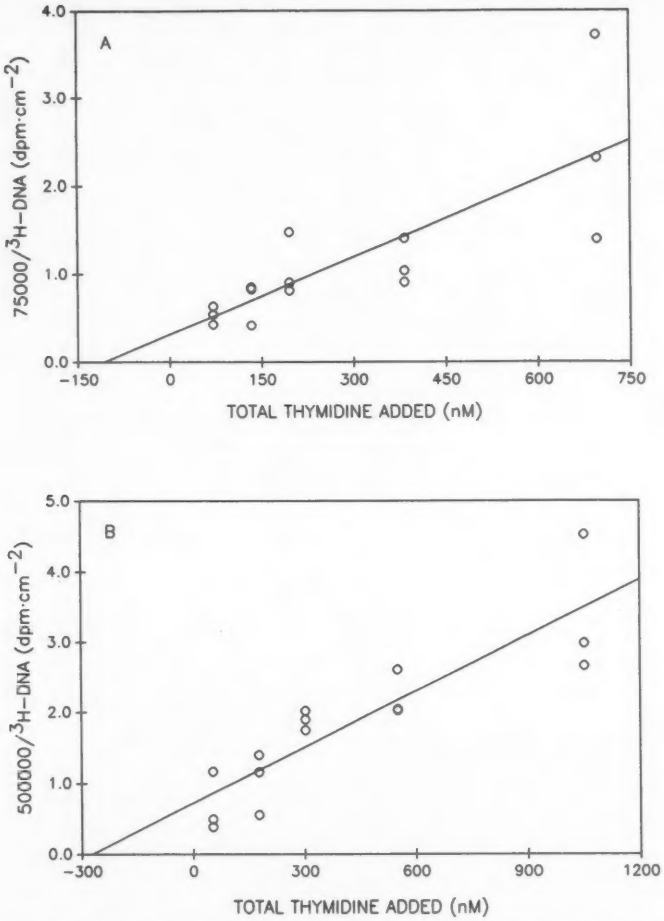

FIG. 3. Isotope dilution plots of incorporation of ^{3}H-TdR into bacterial DNA from the forested site LC on August 2 (A), and from the open site SC on August 4 (B). Each point is an individual sample. The positive horizontal axis is the concentration of labelled and unlabelled TdR added. The intercept with the negative horizontal axis is the effective pool concentration that dilutes the added ^{3}H-TdR. The vertical axis is the reciprocal of radioactivity (DPM in DNA per cm^2 of epilithon).

in the summer. However, these estimates were for the epilithon on the upper surfaces of rocks. Lock et al. (1984) observed epilithic communities on lower rock surfaces, occasionally as great as those on upper surfaces. Therefore, these rates of production were probably a significant underestimate of total bacterial production in the riffles.

Each rock chip was incubated in 8 mL of non-sterile stream water. Water column production (as μg C per 8 mL sample per h, unpubl. data) could represent 1.1, 0.39, 0.17, and 3.8% of the mean epilithic production (as μg C per mean site epilithic chip area per h) at sites CC, LC, WC, and SC, respectively.

Our knowledge of the structure and function of the epilithic bacterial community in streams is growing (for instance, see Rounick and Winterbourn (1983), Lock et al. (1984), and Hamilton (1987)). However, despite the possible importance of this community in running waters, our understanding is still rudimentary (Benke et al. 1988), and production estimates of natural epilithic bacterial communities are not available. A comparison to recent production estimates from artificial or other substrata can, however, be made.

Epiphytic bacteria on snags in Georgian rivers had a mean production of 25 μg C·m^{-2}·h^{-1} over an 18 mo sampling period (Findlay et al. 1986). The production of bacteria, after two months of colonization on unglazed porcelain disks in White Clay Creek, was 0.144–1.04 mg C·m^{-2}·h^{-1} in April in the light (Kaplan and Bott 1989). These rates of production were approximately 10 to 100 times lower than those of this study (range 1.3–51 mg C·m^{-2}·h^{-1}) (Table 1).

Our higher production rates may have been a result of either shorter doubling times, and/or greater bacterial abundance or biomass. However, doubling times from the above studies were equivalent to our shortest times (Table 1). For example, bacteria on riverine snags (Findlay et al. 1986) had a mean doubling time of 8 h (calculated by dividing the mean biomass,

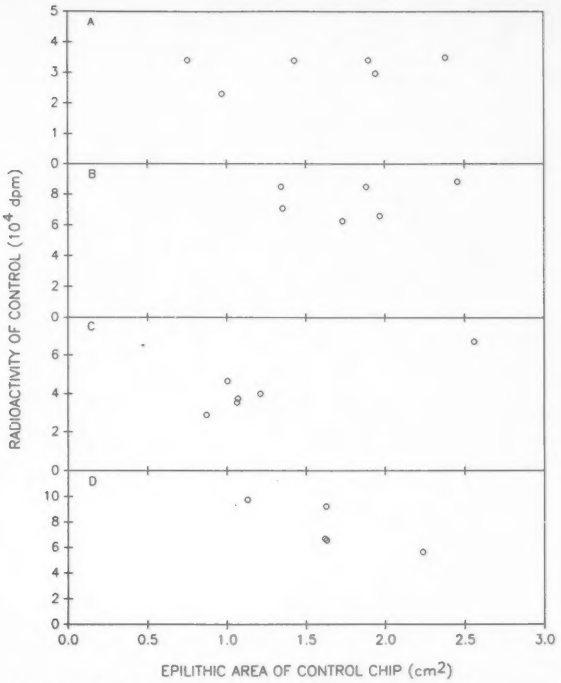

FIG. 4. Radioactivity (DPM, corrected for sample dilution) on control chips as a function of their epilithic area (cm^2). Control chips from production and isotope dilution experiments conducted at sites SC (A), WC (B), CC (C) and SC (D) on June 30, July 12, July 15, and August 4, respectively. One estimate lost from August 4.

0.4 mg $C \cdot m^{-2}$, by the mean production, 25 μg $C \cdot m^{-2} \cdot h^{-1}$). Kaplan and Bott (1989) found doubling times of 3.4–7.2 h on artificial substrata in White Clay Creek. Additional studies report similar doubling times to ours: bacteria on slides immersed in a stream had a doubling time of 2.8–6 h when water temperature was 16.5 to 21°C (Bott, 1975). Epiphytic bacteria on dead salt marsh plants (*Spartina alterniflora*) had a doubling time of 4–69 h (Fallon and Newell 1986). Therefore, our higher production estimates must have been related to a greater bacterial abundance or biomass in the biofilm.

Findlay et al. (1986) and Kaplan and Bott (1989) reported mean bacterial biomass of 0.4 mg $C \cdot m^{-2}$ and 3.3 mg $C \cdot m^{-2}$, respectively (the latter biomass estimate was calculated with a mean cell volume equal to 0.11 μm^3 per call and 1.2×10^{-13} g $C \cdot \mu m^{-3}$ of cell). These estimates were approximately 10–100 times less than those in the present study. In general, as the thickness of the biofilm increases, up to a critical point, the activity of the biofilm should increase (Jeffrey and Paul 1986). Therefore, our higher production estimates are probably reflective of a much thicker biofilm with higher bacterial numbers and biomass.

Results from the new techniques described here indicate that epilithic bacterial production is significant. Application of the technique is not restricted to epilithic stream bacteria; it could be used with other microbial groups on a variety of other aquatic hard substrata. For example, the microbial activities in the biofilm on coral and submerged wood could be measured with this technique. In addition, the methods used for detecting disturbance artifacts and processing laboratory samples can be applied to a variety of other environments, e.g. sediment.

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Effects of Iron Cycling on ^{210}Pb Dating of Sediments in an Adirondack Lake, USA

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In three cores from an acidic lake in the Adirondack State Park of New York, iron cycling accounted for diagenetic enrichment of up to 14% of sediment dry mass. The accuracy of the sediment accumulation rates calculated from the constant rate of supply (c.r.s.) model and the dating and sediment accumulation rates calculated from the constant initial concentration (c.i.c.) ^{210}Pb models were affected by post-depositional movement of iron about the sediment–water interface and through the sediment. Dating biases from iron diagenesis reached as high as 57% and biases to calculated sediment accumulation rates ranged up to approximately 15%. In general, however, the difference between the iron-corrected and uncorrected dating was not much greater than the error expected from routine analytical precision. However, under circumstances of low sediment accumulation rates and high iron enrichment, significant deviations in dating and sediment accumulation calculations for both c.r.s. and c.i.c. ^{210}Pb models may become noteworthy.

Dans les trois carottes étudiées provenant d'un lac acide de l'Adirondack State Park de l'État de New York, les apports en fer contribuaient à l'enrichissement diagénétique des sédiments dans une proportion pouvant atteindre 14%, en poids sec. Le calcul des taux d'accumulation des sédiments effectué au moyen du modèle fondé sur un taux d'accumulation constant de même que la datation et le calcul des taux d'accumulation effectué au moyen des modèles utilisant le ^{210}Pb et une concentration initiale constante perdaient en précision à cause des déplacements du fer à l'interface eau-sédiment et à travers les sédiments. Le pourcentage d'erreur sur la datation attribuable à la diagenèse du fer pouvait atteindre 57% et celui sur les taux d'accumulation, environ 15%. En général, cependant, la différence entre les valeurs de datation corrigées et non corrigées, relativement au biais attribuable au fer, donnait un pourcentage d'erreur ne dépassant pas beaucoup celui obtenu avec les méthodes courantes d'analyse. Cependant, quand les taux d'accumulation de sédiments sont faibles et que l'enrichissement en fer est important, le pourcentage d'erreur dans la datation et le caclul des taux d'accumulation des sédiments au moyen des deux types de modèle mentionnés plus haut peuvent devenir importantes.

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Contamination of the natural environment by anthropogenic pollutants has typically occurred over time spans much greater than those over which we have been able to monitor and assess the impacts of pollutants. There are, however, methods which allow for approximate reconstruction of historical events affecting lakes. These methods focus on lake sediments, which may preserve records of lake and watershed responses to pollutants.

Sediment chronology may be established using varves (Tolonen and Jaakkola 1983), the analysis of radioactive decay products, such as ^{210}Pb (Robbins 1978; Binford 1984) or ^{237}Cs (Pennington 1981), mineral magnetism (Oldfield et al. 1983; Anderson 1986), and by the correlation of sedimentary pollen or charcoal with historical records of local logging or fires (Charles and Norton 1986). Once a relationship has been established between sediment depth and time before present, careful analysis of selected sediment constituents may yield detailed information about the history of pollutant inputs into watersheds.

Dating lake sediments by means of ^{210}Pb analysis has become popular because ^{210}Pb's half-life of 22 yr allows for finely resolved dating of approximately 150–200 yr of accumulated sediment.

There are two common methods of calculating ^{210}Pb dates under conditions of varying sediment accumulation. Both the constant rate of supply (c.r.s., Appleby and Oldfield 1978) and the constant initial concentration (c.i.c.) models use a relatively simple form of a first-order exponential decay function:

$$(1)\quad \text{(c.r.s.)}\ t_i = (1/k) * (A_o / A_i)$$

$$(2)\quad \text{(c.i.c.)}\ t_i = (1/k) * \ln (C_o / C_i)$$

where:

t_i = Age at base of interval i, and

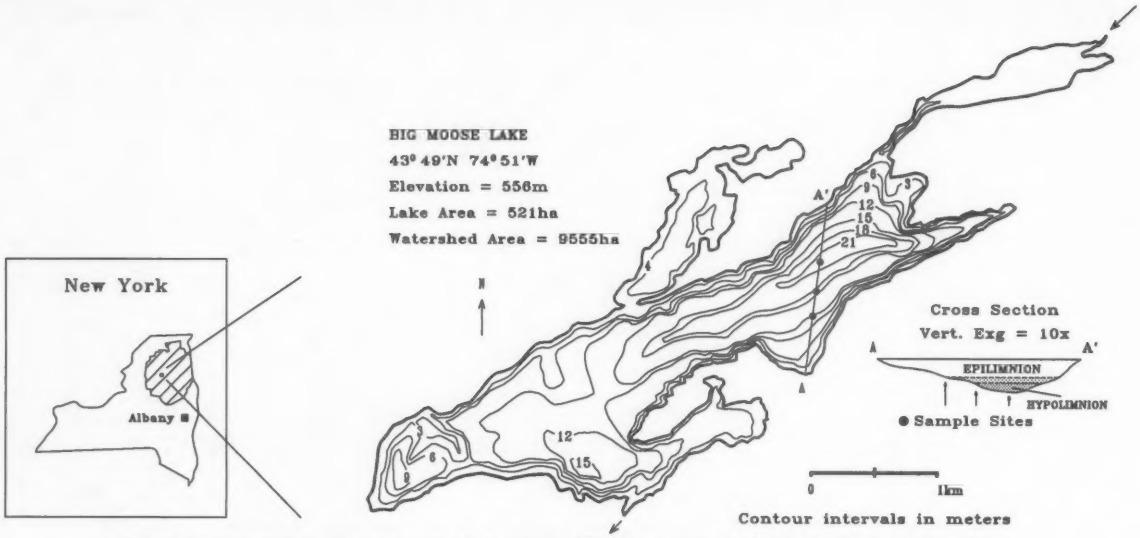


FIG. 1. Location bathymetry and sample site locations of Big Moose Lake, Adirondack State Park, New York.

k = First-order decay constant for ^{210}Pb (0.03114·yr^{-1}).

The basic difference between the c.r.s. and c.i.c. models is in the use of ^{210}Pb activity in the terms:

c.r.s.: A_o = Total cumulative unsupported ^{210}Pb, pCi·cm^{-2} (measured as an integrated accumulation of unsupported ^{210}Pb through the length of the core)

A_i = Cumulative unsupported ^{210}Pb at interval i, pCi·cm^{-2}.

c.i.c.: C_o = Unsupported ^{210}Pb at sediment surface, pCi·g^{-1} (typically derived from a linear regression of the natural log of unsupported ^{210}Pb vs. depth of interval i).

C_i = Unsupported ^{210}Pb at interval i, pCi·g^{-1}.

Once sediment intervals have been dated by either the c.i.c. or c.r.s. model, net sediment accumulation rates (g·cm^{-2}·yr^{-1}) may be obtained by dividing the cumulative dry weight of sediment by the age of the interval.

The sampling and analytical precision for ^{210}Pb dating can be satisfactorily estimated, but the accuracy of results from the c.r.s. and c.i.c. models depends upon the validity of their assumptions. In the c.i.c. model, it is assumed that deposition of other sediment constituents (non ^{210}Pb-labeled material) does not significantly affect the initial ^{210}Pb concentration (C_o), which is normalized for the dry mass of sediment. In the c.r.s. model, unsupported ^{210}Pb activity is normalized per unit area of lake bottom (pCi·cm^{-2}), but is ultimately calculated from the dry mass activity as:

$$(3)\quad A_o = \Sigma\, C_i * P_i * d_i$$

where:

C_i = pCI ^{210}Pb·g^{-1} dry sediment for interval i,
p_i = g dry sediment·cm^{-3},
d_i = thickness of interval i (cm).

Since parameters used in both models are directly related to sediment mass, post-depositional changes in sediment composition may affect the accuracy of the calculated sediment accumulation rates and in the case of the c.i.c. model, the dating itself.

Iron cycling is one process which may gradually change sediment mass after initial burial. In this paper we will examine the effect of iron enrichment in surficial sediment on the ^{210}Pb c.r.s. and c.i.c. model calculations. We hypothesize that iron cycling will affect the accuracy of sediment accumulation rates calculated from the c.r.s. model, c.i.c. dates, and c.i.c. sediment accumulation rates (Equations 2 and 3).

Methods

Porewater, sediment, and water column sampling was conducted at Big Moose Lake, located in the headwaters of the North Branch of the Moose River (NBMR). Detailed descriptions of the NBMR drainage system may be found elsewhere (Driscoll and Newton 1985; Driscoll et al. 1987). Water column, sediment, and sediment porewater samples were collected at 12-, 17-, and 24-m depth stations within Big Moose Lake (Fig. 1) during a 2 wk period in July of 1985. The porewater sampler buoy marker was used as the primary datum for positioning the piston and gravity core samplers, and water column sampler. Each sample was taken as close as possible to the designated site (within approximately 10 m) to minimize spatial variability, while also minimizing the possible disturbance of other sampling procedures.

The porewater within the Big Moose Lake sediment at each site was sampled by in-situ dialysis using a device similar to the sampler described by Hesslein (1976). A stabilizing platform was added to the basic design to provide clear designation of the sediment–water interface (Gubala 1988). The platform was positioned to allow 12 1-cm (8.5 cm^3 vol) dialysis cells to sample the water column and 48 1-cm cells to penetrate into the sediment. The plexiglas sampler was fitted with a 0.2 μm Nuclepore dialysis membrane approximately 48 h prior to installation. The unit was then submerged in deionized water and purged with N_2 gas to remove oxygen from the sampler (Carignan 1984; Carignan et al. 1985) and remained in deoxygenated water until the time of installation. The unit was

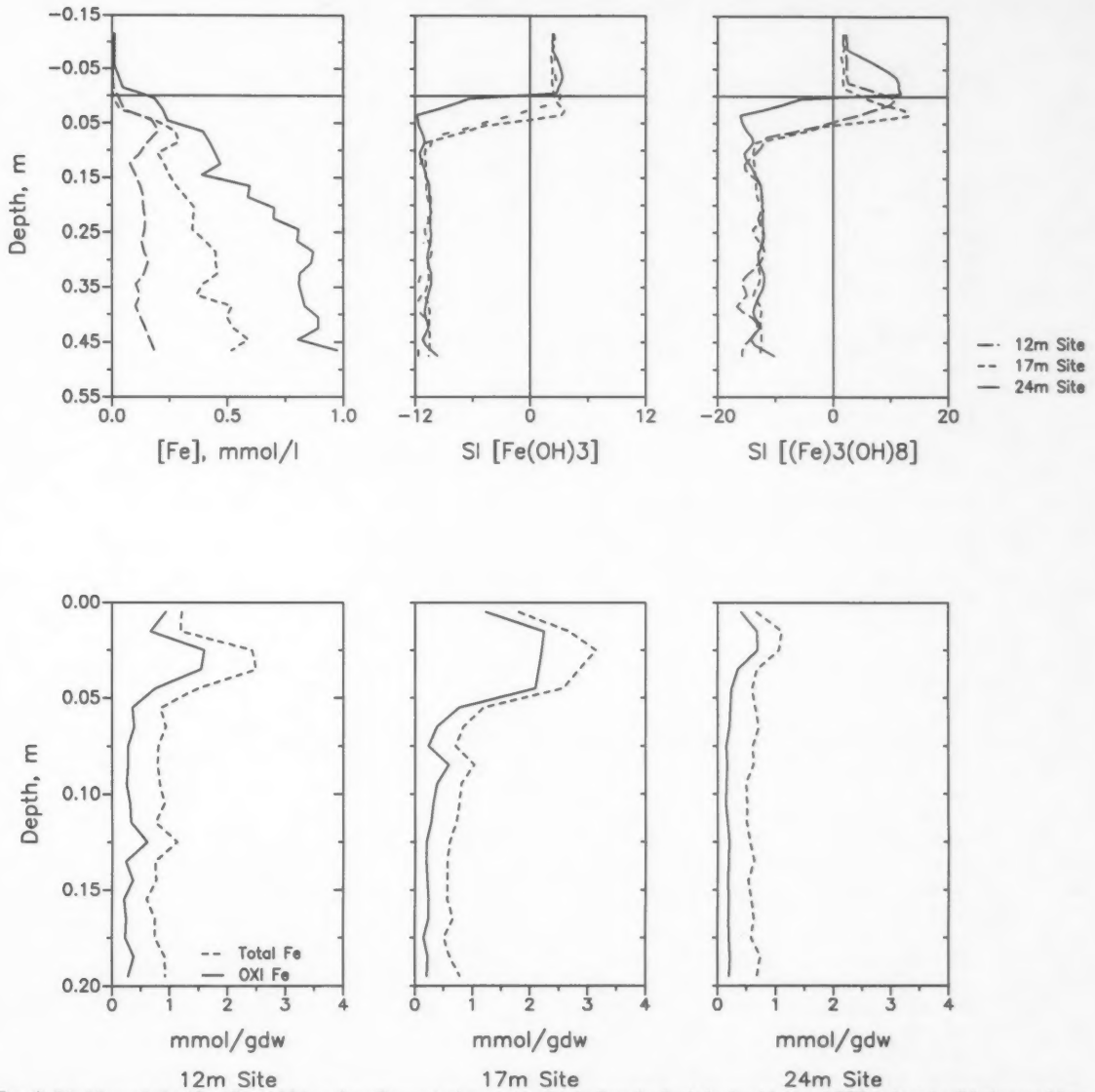


FIG. 2. Big Moose Lake 12-, 17-, and 24-m sites: Porewater iron, saturation indices for ferric hydroxides, and OXI and total solid phases of iron.

installed by SCUBA divers and allowed to equilibrate for a period of 15 d (Carignan 1984). Once the sampler was retrieved, aliquots from each cell were quickly removed and preserved appropriately for subsequent analyses (major ions, trace metals, dissolved inorganic and organic carbon; Gubala 1988). Since sample size was small, soluble iron could not be chemically speciated between ferrous and ferric forms. However, due to the distinctly different nature of the water column and porewater environments as characterized by the concentration of electron acceptors (SO_4, NO_3, O_2), it was assumed that all iron within the porewater existed in the ferrous form. The iron species within the water column was determined by thermodynamic modelling, using O_2 and pH to fix pE (Gubala 1988). Diffusive flux rates of chemical constituents were calculated based upon the coefficients presented by Li and Gregory (1974) and the technique recommended by Lasaga (1979).

Sediment from gravity cores (surface area = approx. 40 cm^2, depth) was used exclusively for metals speciation. The sediment from these cores was immediately sectioned into 1-cm thick intervals to a depth of 20 cm. To avoid chemical alteration of sediment caused by exposure to atmospheric oxygen (Rapin et al. 1986), sectioning of the core was performed in a glove box under a N_2 gas environment. Sediment sections were then subjected to a sequential extraction procedure for the speciation of Fe (Tessier et al. 1979) within 24 h of collection. The extraction procedure consisted of five operationally defined fractions. The five fractions were summed to calculate the total metals concentration. The most noteworthy fraction of iron discussed

TABLE 1. Porewater Fe fluxes and accumulation rates of solid phase Fe from the 12-, 17-, and 24-m sites at Big Moose Lake. D_z = mean one-dimensional diffusive flux rate of Fe corrected for temperature, porosity and estimated torturosity.

Site depth	12-m	17-m	24-m
Porewater iron:			
D_z, $\mu mol \cdot cm^{-2} \cdot yr^{-1}$			
Across the sediment–water interface (−0.03 to 0.03 m)	2.05	1.60	3.92
Through the sediment (0.00–0.45 m)	0.51	1.22	2.21
Solid phase iron:			
Maximum total accumulation rate, $\mu mol \cdot cm^{-2} \cdot yr^{-1}$	18.0	57.4	21.0
Baseline OXI accumulation rate, $\mu mol \cdot cm^{-2} \cdot yr^{-1}$	4.2	9.4	13.2
Peak OXI Iron Enrichment rate, $\mu mol \cdot cm^{-2} \cdot yr^{-1}$	11.4	40.5	4.5

TABLE 2. ^{210}Pb parameters and sediment accumulation rates for cores from the 12-, 17-, and 24-m sites at Big Moose Lake.

Site depth	12-m	17-m	24-m
Cumulative unsupported ^{210}Pb activity, $pCi \cdot cm^{-2}$	10.59	17.30	20.58
Surface activity (C_o) supported ^{210}Pb, $pCi \cdot g^{-1}$	0.60	0.36	0.70
Mean c.r.s. model sediment accumulation rate, $g \cdot cm^{-2} \cdot yr^{-1}$	0.007	0.020	0.025
Mean c.i.c. model sediment accumulation rate, $g \cdot cm^{-2} \cdot yr^{-1}$	0.006	0.017	0.017

in this paper is "oxyhydroxide," (OXI) derived from a 6 h extraction with 0.04M NH_2OH HCl in 25% (v/v) HOAc. The OXI phase of iron is considered to represent a mixture of amorphous precipitates best described in the available thermodynamic literature as forms of ferric oxyhydroxides (e.g. $Fe(OH)_3$ and $(Fe_3(OH)_8)$. Extraction reagents were deoxygenated with N_2 gas prior to use and all sediment processing was conducted within the N_2 purged glove box.

Sediments were also analyzed for excess ^{210}Pb activity to determine age and sediment accumulation rates for the past 200 yr. ^{210}Pb was measured at 16 depth intervals by measuring its equilibrated grand-daughter product ^{210}Po with ^{208}Po added as an internal yield tracer. The polonium isotopes were distilled from a 0.4–3.0 g dry sediment at 550°C following pretreatment with concentrated HCl and plated directly (without NHO_3 oxidation) onto silver planchettes from a 0.5N HCl solution (modified from Eakins and Morrison 1978). Activity was measured with Si-depleted surface detectors and an Ortec Adcam™ alpha spectroscopy system. Unsupported ^{210}Pb was calculated by subtracting supported activity from total activity measured at each level; supported ^{210}Pb was estimated from the asymptotic activity at depth (the mean of the lowermost samples in each core). Dates and sedimentation rates were determined according to the c.r.s. and c.i.c. models (Appleby and Oldfield 1978) with confidence intervals calculated by first-order error analysis of counting uncertainty.

Further details of the methods of sampling and analysis used in this study are given by Gubala (1988).

Results

Differences in the concentrations and calculated fluxes of porewater iron (Fig. 2, Table 1) were observed between sites. The 24-m site showed the highest porewater concentrations (max = 0.94 $mmol \cdot L^{-1}Fe$) and the potential for the most rapid diffusion of soluble iron through the sediment porewater (2.21 $\mu mol \cdot cm^{-2} \cdot yr^{-1}Fe$) and across the sediment-water interface (3.92 $\mu mol \cdot cm^{-2} \cdot yr^{-1}Fe$).

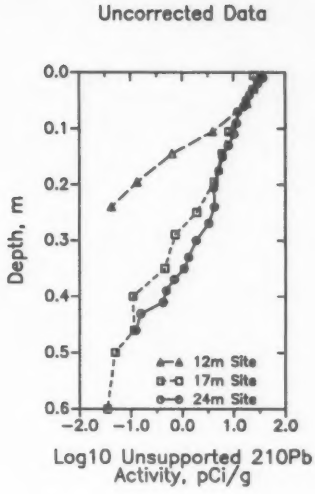
A computer program for the calculation of chemical equilibrium composition of aqueous systems, MINEQL, (Westall et al. 1976), was used to determine the saturation indices (SI = LOG10 (Q_{so}/LOG10($^*K_{so}$)) for important iron solid phases. Values of SI less than 0 indicate undersaturation with respect to a given mineral phase, while positive values suggest a condition of supersaturation with the potential for precipitation of the mineral phase. All sites within Big Moose Lake were undersaturated with respect to $Fe(OH)_3$ and $(Fe)_3(OH)_8$ (($LOG10(^*K_{so})$ = 3.00 and −6.42 respectively; Robie et al. 1978) at depth in the sediment (SI < −10), and oversaturated with respect to the same mineral phases near the sediment–water interface and within the water column (SI > +3, Fig. 2). However, the point of maximum supersaturation differed among sites, with the 17-m site showing most pronounced subsurface maxima with respect to both solid phases.

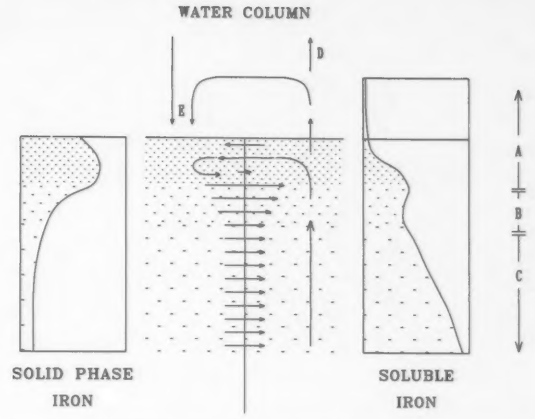
Solid phases of iron at all sites were dominated by an "oxyhydroxide" fraction (OXI, Fig. 2). Maximum concentrations of iron "hydroxides" (OXI) were found at each site at approximate depths of 2- to 5-cm (1.60, 2.24, 0.69 $mmol \cdot gdw^{-1}$ Fe for the 12-, 17-, and 24-m sites respectively). The maximum thickness and concentration of OXI iron varied between sites with the greatest maximum occurring at 17-m (approx. 5-cm). Elevated OXI iron concentrations corresponded with the regions of supersaturation of $Fe(OH)_3$ and $(Fe)_3(OH)_8$.

Porewater concentration gradients indicated that iron may have been diffusing upward and out of the sediment at the 24-m site, and upward to just below the sediment-water interface at the 17- and 12-m sites (Fig. 2). The presence of soluble iron above the sediment-water interface at the 24-m site was likely due to the absence of other electron acceptors (SO_4, NO_3) in the electron rich environment (Gubala 1988; White et al. 1989). Saturation indices of ferric hydroxides showed a zone of supersaturation within a few centimeters of the sediment–water interface at all sites. These data suggested that the soluble iron diffusing upward through the sediment column may have been oxidized and precipitated as solid phase iron oxyhydroxides near the sediment–water interface. The observed surface enrichment of OXI iron at each site supported this hypothesis. Wilson et al. (1986) described a similar "oxidation front" mechanism on the Madeira Abyssal Plain, where iron was oxidized with pelagic sediments by molecular oxygen diffusing into the sediment from above.

Cumulative unsupported ^{210}Pb activity increased with site depth from 10.6 $pCi \cdot cm^{-2}$ at 12-m to 20.6 $pCi \cdot cm^{-2}$ at 24-m (Table 2). The 24-m site showed the fastest apparent rate of sediment depth of 20-cm at the 24-m site corresponded to a c.r.s. date of 1930 and a c.i.c. date of 1916, whereas the 20-cm intervals of the 17- and 12-m sites corresponded to c.r.s. dates of 1908 and 1779, and c.i.c. dates of 1918 and 1782 respectively.

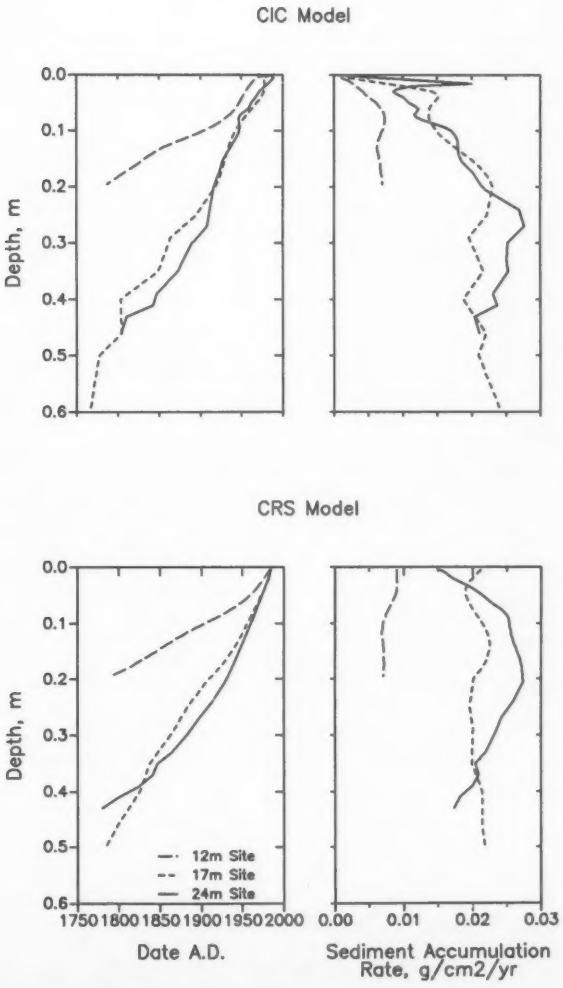
Dating and sediment accumulation curves, derived from the c.i.c. and c.r.s. models for uncorrected data (Fig. 3) were roughly in agreement. Sediment accumulation at the 12-m site





A. Region of Iron Oxihydroxide Precipitation
B. Region of Enhanced Iron Solid Phase Dissolution
C. Region of Slow Solid Phase Dissolution
D. Diffusive and/or Advective Removal of Soluble Iron
E. Sedimentation of Solid Phase Iron

FIG. 4. Conceptual model of the genesis of iron oxidation fronts in lake sediments.



was noticeably slower than the 17- and 24-m sites (Fig. 3), presumably due to the focusing of ^{210}Pb-labeled fine sediments within the deeper regions of the lake (Davis and Ford 1982). However, c.i.c. dating yielded a sediment accumulation curve for the 12-m site that decreased sharply between 0.05 m and the surface, while the c.r.s. accumulation rates remained unchanged. Similar, but less conspicuous discrepancies between c.i.c. and c.r.s. model accumulation rates were noted for the 17- and 24-m sites. The sediment accumulation profiles for these sites were roughly similar between models with the exception of the region near the sediment surface of the sediments. In this region, the c.i.c. model produced sharp changes in the calculated accumulation rates, where c.r.s. values remained relatively uniform. The sharp changes in c.i.c. accumulation rates for each site are likely artifacts of the calculation methods. Because C_o for the c.i.c. model was derived by linear regression of $\ln(C_i)$ vs. depth with equal weighting of the raw data, the surface values for C_i may not sufficiently influence the calculation of the regression intercept, which is used to calculate interval ages. It is possible for c.i.c. dating to yield negative age estimates for the first interval(s) when the regression yields a value of C_o that is smaller than C_i. Negative, or disproportionately small age estimates for the first few intervals have a pronounced effect upon calculated rates of sediment accumulation.

Discussion

Iron Diagenesis

The accumulation rates of OXI iron in the sediment at each site showed near-surface peaks that could be attributed to a

FIG. 3. Big Moose Lake 12-, 17-, and 24-m sites: Uncorrected unsupported ^{210}Pb, c.i.c. and c.r.s. model dates and sediment accumulation rates.

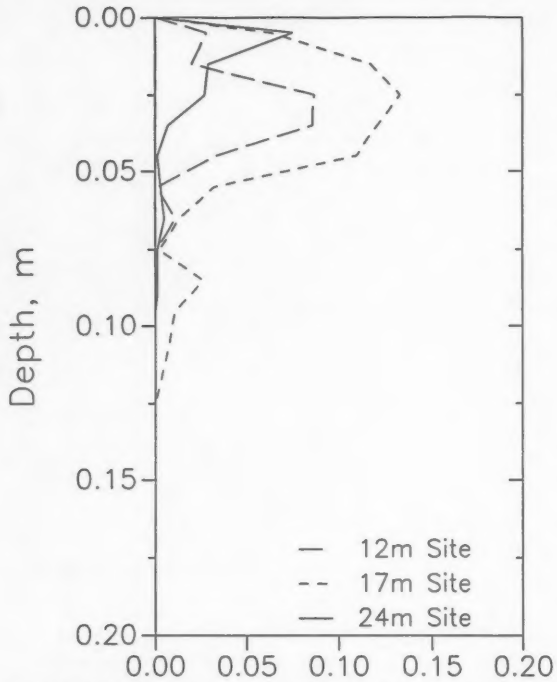


FIG. 5. Big Moose Lake 12-, 17-, and 24-m sites: Iron enrichment factors.

theoretical oxidation front mechanism (Gubala 1988). Baseline accumulation rates of OXI iron in Big Moose Lake sediment were determined from down-core iron accumulation rates by a least squares statistical approach (Table 1). The baseline values for OXI iron (4.2, 9.4, 13.2 $\mu mol \cdot cm^{-1}$ yr for the 12-, 17-, and 24-m sites respectively) increased with site depth, consistent with the trends expected to result from sediment focusing (Wetzel 1975). Subtracting the baseline values from the observed accumulation rates for OXI iron resulted in calculated peak enrichments (Table 1). The maximum rates at which OXI iron accumulated within the sediment were greater than the calculated diffusive fluxes of soluble iron through the sediment and across the sediment–water interface (Table 1). Thus, the observed accumulation rates of OXI iron must have resulted from a combination of long term recycling of soluble iron about the point of enrichment combined with an upward diffusive flux of soluble iron from depth in the sediment (Fig. 4). The former process would maintain peak iron concentrations within the appropriate redox regime while the latter could affect the amplitude of that cycle. The presence of iron enriched regions within the first few centimeters of sediment also indicate that iron precipitation reactions in these environments must be kinetically faster than the dissolution reactions (Stumm and Morgan 1981). If the reverse were true, only thin (mm thickness) surficial bands of enriched iron would be expected.

The distributions of iron among different solid phases may change significantly after initial deposition. Responding to depth-dependent redox conditions, iron was vertically displaced to some degree within each of the cores from Big Moose Lake. Since the labile fractions of iron may be susceptible to postdepositional movement, depth profiles should not be interpreted as representing changes in historical deposition events.

Porewater gradients of soluble iron and surface enrichment of solid phase iron have been observed in other aquatic systems. Carignan and Nriagu (1985) presented porewater and solid phase iron data for Clearwater (mean pH 4.5) and McFarlane (mean pH 7.5) Lakes near Sudbury, Ontario. Porewater concentration gradients indicated the potential for diffusive flux of iron upward through the sediment in both lakes. Total iron showed significant surface enrichment within the three sediment cores from Clearwater Lake and the sediment core from McFarlane Lake. The ranges of porewater and solid phase iron from both lakes were remarkably similar to those from the Big Moose Lake sites. Similar evidence for diagenetic enrichment of iron via porewater diffusion and mineral precipitation was presented by Davison (1981; Esthwaite Water, UK), Sakata (1985; T Reservoir, Japan), Cornwell (1986; Toolik Lake, Alaska) and Wilson et al. (1986; Madeira Abyssal Plain). Pronounced surface enrichments of OXI iron were also noted in the sediment cores from another site in Big Moose Lake and in nearby Dart Lake and Lake Rondaxe (Gubala 1988). Therefore, although this study focuses on one set of cores from Big Moose Lake, Diagenetic remobilization of iron in surficial sediments is likely to be a common phenomenon in other aquatic systems as well.

Corrections of ^{210}Pb Dating from Iron Remobilization Estimates

Diagenetic processes resulting in iron oxidation fronts increased the dry solid mass of sediment within the first few centimeters of each core from Big Moose Lake. All constituents that were measured on a gram–dry–weight basis were subsequently biased by the postdepositional enrichment or depletion of iron from biochemical recycling. Constant initial concentration and c.r.s. dating and sediment accumulation rates were also affected by the redistribution of iron in the sediment.

Since mechanisms of iron diagenesis are related to the chemical speciation of solid phases (e.g. OXI phases), it was possible to correct the observations that were based upon dry sediment mass for iron redistribution. The first step in this process was to quantify the degree of iron enrichment in the cores. Baseline concentrations of OXI iron were determined by a modified iterative least squares analysis of the bottom sediments of each core. The mean and variance of OXI iron concentrations from the 0.20–0.18 m intervals were determined first. Additional data points were then added in sequence, and the new mean and variance were calculated after each iteration. The point of minimum variance about the mean was used as the baseline value for OXI iron. These values were then subtracted from their respective OXI iron profiles and converted to mass proportions (Fig. 5). The proportional enrichment factors were used to correct the unsupported ^{210}Pb activities, c.r.s. and c.i.c. dates, and sediment accumulation rates.

Results from the uncorrected c.r.s. model routinely underestimated the age of the lowermost intervals at the 12- and 17-m sites (24 and 18% respectively; Fig. 6). Accordingly, sediment accumulation rates deviated somewhat between the iron corrected and uncorrected cases. The c.r.s. dating of the 24-m site was unaffected by iron enrichment, presumably because peak iron enrichment was low and the sediment accumulation rates were relatively high.

The manner in which c.r.s calculations were performed (e.g. integrated activity from the base of the core) apparently reduced

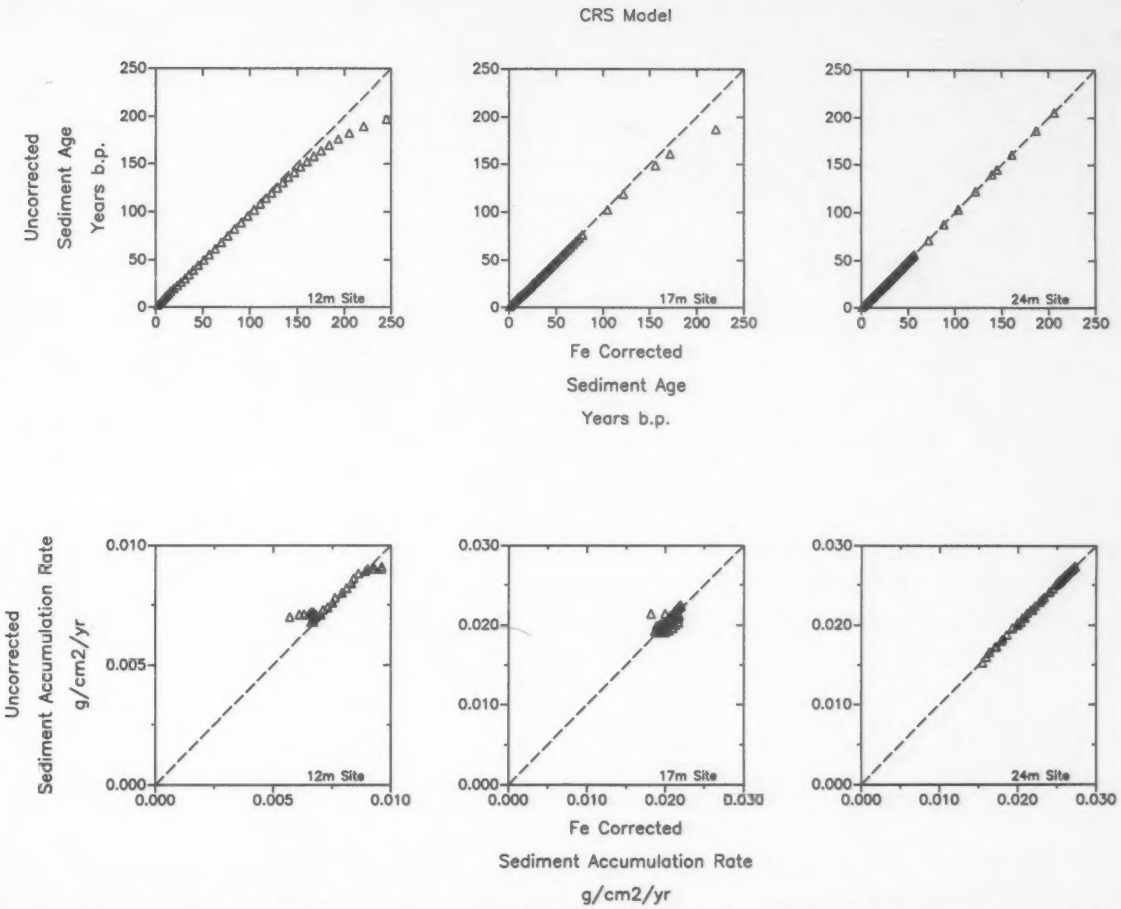


FIG. 6. Big Moose Lake 12-, 17-, and 24-m sites: Uncorrecteed versus iron corrected c.r.s model sediment ages and sediment accumulation rates.

the effects of iron enrichment. The dilution of the unsupported ^{210}Pb activity was reciprocally matched by the mass addition of iron to the cumulative mass of the sediment. Dates and sediment accumulation rates in the uppermost intervals remained in close agreement between the iron-corrected and uncorrected cases, because those results were based upon the integrated ^{210}Pb from all the lower intervals. The discrepancies between the iron-corrected and uncorrected cases in the lower-regions of two of the sites were the result of the small amount of integrated ^{210}Pb remaining at depth.

A major systematic deviation between uncorrected and iron-corrected c.i.c. dates and sediment accumulation rates was noted for the 17-m site, where iron enrichment was the greatest (Fig. 7). At that site, the uncorrected c.i.c. results underestimated the interval ages by a mean of approximately 10% throughout the length of the core. This bias caused a routine overestimation of the c.i.c. sediment accumulation rates. The c.i.c. results from the 12- and 24-m sites did not deviate significantly between iron corrected and uncorrected cases (<3%).

Because c.i.c. model dating depends upon the discrete activity of unsupported ^{210}Pb at the surface (C_o) and at each interval (C_i), rather than an integrated value, it was surprising to find that the results for the uncorrected and iron-corrected cases were in good agreement for two of the three sites. The congruence for the 12- and 24-m sites was due to a coincidental balancing of the linearly regressed C_o with those of the down-core values of C_i for each interval. At the 17-m site, however, iron enrichment in the first 10-cm was sufficient to skew the regression of C_i vs. depth and produce a systematic underestimation of the age of each down-core interval.

The significance of iron enrichment in biasing the c.r.s. and c.i.c. ^{210}Pb calculations can best be assessed by comparison with the analytical precision of ^{210}Pb measurements. After propagating the analytical error through the dating calculations (Table 3), it was apparent that the biases resulting from iron diagenesis were generally no greater than those errors resulting from standard analytical precision. The one exception came in the c.i.c. results for the 17-m site. Iron cycling at the 17-m site was sufficiently pronounced to produce an age bias approximately three times greater than the analytical error.

Conclusions

Iron was enriched within the surficial sediments of Big Moose Lake by the combined process of diffusion, redox transformations, and precipitation reactions. In general, mass dilution of the sediment by iron enrichment only modestly biased the dating of Big Moose Lake sediments. The differences between

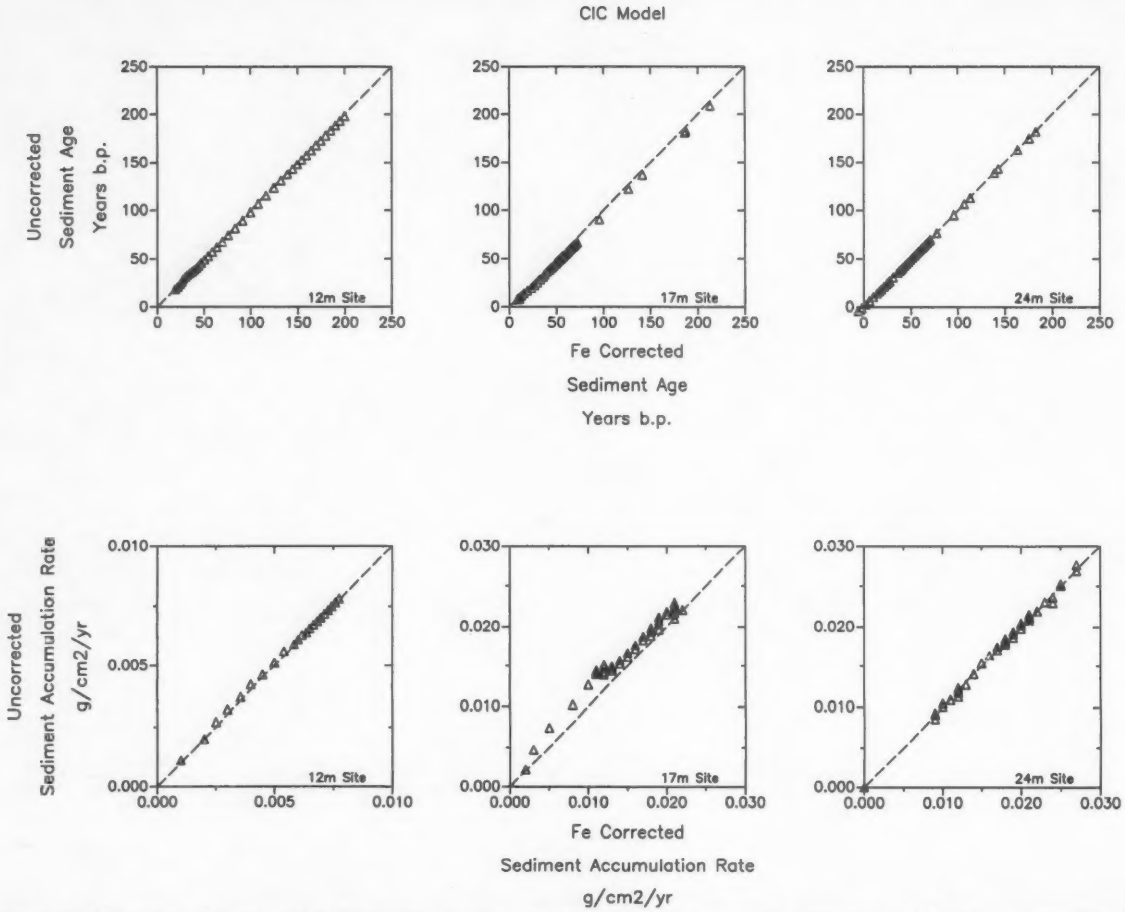


FIG. 7. Big Moose Lake 12-, 17-, and 24-m sites: Uncorrected versus iron corrected c.i.c. model sediment ages and sediment accumulation rates.

TABLE 3. Percent error for uncorrected iron biased c.r.s. and c.i.c. calculations (FeERR)[a] and the coefficient of analytical variance (CAV)[b] from the 12-, 17-, and 24-m sites at Big Moose Lake.

	Site 1, 24-m			Site 2, 17-m			Site 3, 12-m		
	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
c.r.s. Age:									
FeERR	0.5	0.1	1.5	3.3	0.5	17.8	4.5	0.1	24.1
CAV	3.1	0.8	5.2	3.4	0.7	24.4	3.6	1.0	10.5
c.i.c. Age:									
FeERR	3.1	0.2	57.7	10.1	2.3	27.0	1.9	0.1	4.2
CAV	4.3	1.0	13.8	2.3	0.8	10.2	7.6	3.2	18.1

[a]((Uncorrected Calculations)/(Iron Corrected Calculations))*100, $n = 20$.
[b]((Standard Deviation)/(Mean))*100, $n = 20$.

the iron-corrected and uncorrected dating was approximately equal to the error expected from routine analytical variation. However, under circumstances of low sediment accumulation rates and high iron enrichment, iron enrichment may have a consequential effect upon ^{210}Pb dating and the calculation of sediment accumulation rates.

The accuracy of any sediment dating technique, normalized to dry sediment mass, should be carefully evaluated in low sedi-

mentation-rate environments which show evidence of post-depositional movement of iron or other diagenetically active materials.

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Occurrence, Size, and Sexual Maturity of Long-Finned Squid (*Loligo pealei*) at Nova Scotia and Newfoundland, Canada

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Dawe, E. G., J. C. Shears, N. E. Balch, and R. K. O'Dor. 1990. Occurrence, size, and sexual maturity of long-finned squid (*Loligo pealei*) at Nova Scotia and Newfoundland, Canada. Can. J. Fish. Aquat. Sci. 47:1830–1835.

A major extension of the geographic range of *Loligo pealei*, in quantitative as well as spatial aspects, is described. The species' range is extended northward and eastward to approximately 47°30'N: 53°06'W, based on its occurrence in Newfoundland inshore trap samples in the autumn of 1986. Biological data from these samples, as well as from collections from Nova Scotian inshore traps from 1974 to 1986, indicate that *L. pealei* becomes sexually mature and spawns in Nova Scotian waters but not at Newfoundland. *Loligo pealei* appears to be prevalent in Canadian waters at times when its sympatric competitor, the short-finned squid *Illex illecebrosus*, is not abundant. The reported catch of *L. pealei* in Atlantic Canada for 1986 was 67 t, which suggests that this species could possibly support a small Canadian fishery in some years.

Un prolongement important, tant sur le plan quantitatif que spatial, de l'aire de distribution de *Loligo pealei* est décrit. D'après les captures faites au moyen de trappes sur la côte de Terre-Neuve à l'automne 1986, l'aire de cette espèce s'étend vers le nord et vers l'est jusqu'à environ 47°30'N: 53°06'0. Selon les données biologiques tirées de ces échantillons, de même que d'échantillons recueillis à la trappe sur la côte de la Nouvelle-Écosse, *L. pealei* atteint sa maturité sexuelle et fraie dans les eaux de la Nouvelle-Écosse, mais pas à Terre-Neuve. On retrouve cette espèce en assez grande quantité dans les eaux canadiennes quand l'encornet, *Illex illecebrosus*, une espèce sympatrique avec laquelle elle entre en compétition, y est peu abondante. En 1986, on a enregistré des captures de 67 t de *L. pealei* au Canada atlantique, ce qui laisse penser que cette espèce pourrait éventuellement soutenir une pêche commerciale réduite.

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The accepted limits of the geographic distribution of the neritic squid *L. pealei* (LeSueur) extend along the Continental Shelf as far south as the Gulf of Venezuela, and as far north as Cobequid Bay in the Bay of Fundy (Fig. 1) and Brown's Bank (Bigelow 1924; Stevenson 1934; Mercer 1970; Lange 1980; Lange and Johnson 1981; Summers 1983). However, the species occurrence near Brown's Bank is based on very few samples (Lange and Johnson 1981). Unfortunately, squid catch statistics in the areas around New Brunswick, Nova Scotia, and Newfoundland (NAFO Subareas 3 and 4, Fig. 1) have not always differentiated between the two major species *I. illecebrosus* and *L. pealei*, so there are no historical data for examining possible interactions between the two populations in Atlantic Canadian waters.

This paper reports on the extension of the northern and eastern limits of the geographic distribution of *L. pealei*, based on specimens collected from inshore waters of Newfoundland in 1986 and of Nova Scotia in 1974, 1975, 1976, 1979, 1981, 1985, and 1986. The first description of the biological characteristics of *L. pealei* from Newfoundland and eastern Nova Scotia is also outlined in this paper. A possible relationship between *L. pealei*'s range extension and the dramatic decline in the *I. illecebrosus* population from its peak in 1979 is also speculated upon.

Materials and Methods

During research in Newfoundland and Nova Scotian waters on the ommastrephid squid, *I. illecebrosus*, the major species normally found in the area, small incidental collections were also made of the loliginid squid *L. pealei*. Fourty-four *L. pealei* were collected in a box trap at Holyrood, Newfoundland (Fig. 1) between September 2 and October 14, 1986. An additional specimen was collected in a box trap at Dildo, Newfoundland on September 10, 1986. Collections were also obtained from box traps in St. Margaret's Bay and Herring

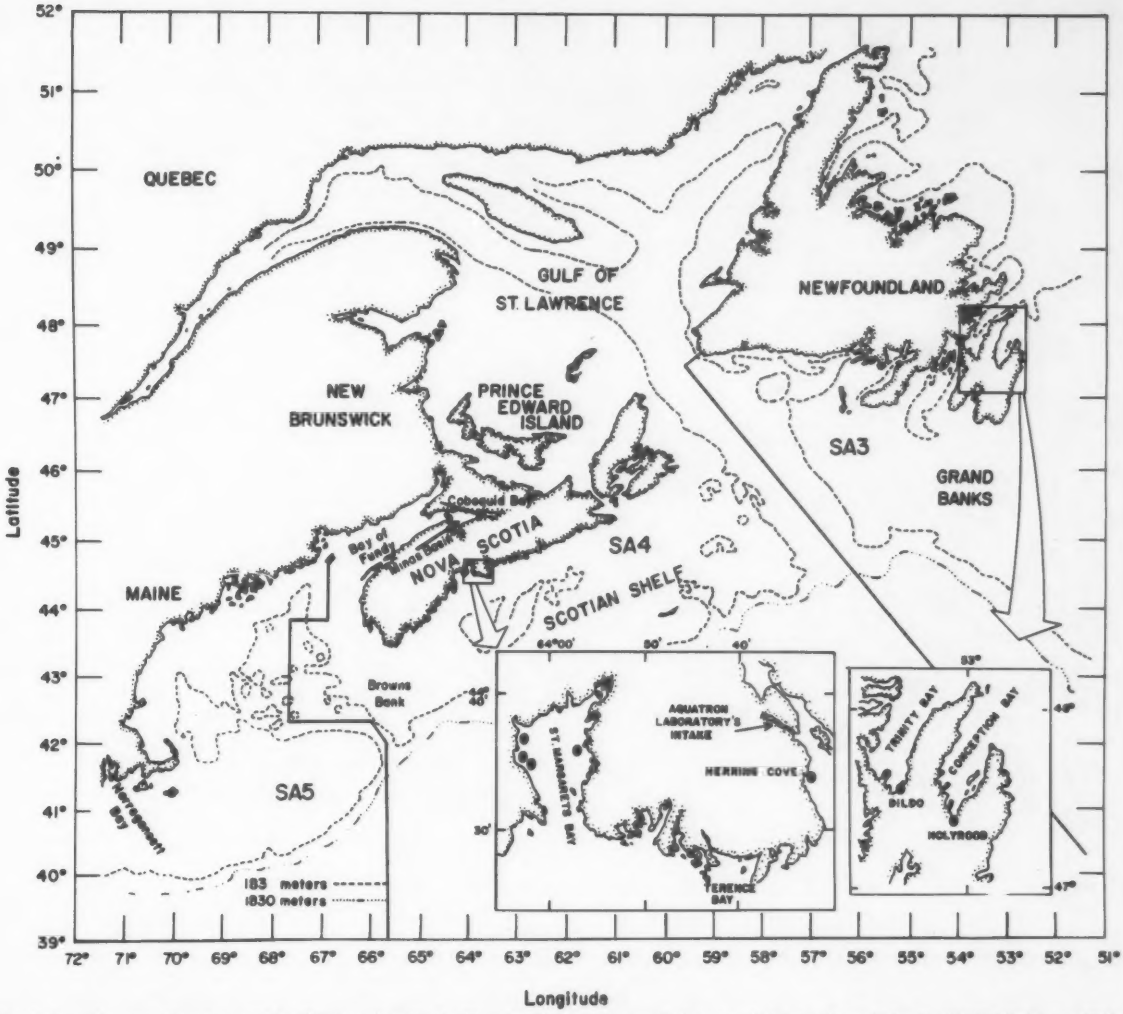

FIG. 1. Location map showing squid collection sites (dark ellipses) and the Aquatron Laboratory's intake, boundaries for NAFO Subareas (SA) 3–5 (dark lines) and other place names referred to in the text.

Cove, Nova Scotia (Fig. 1) during August 12–September 17, 1974; June 17–27, 1975; June 24, 1976; June 2, 1979; August 27, 1981; October 25, 1985; and September 19–October 15, 1986. In contrast with Newfoundland, the objective of research at Nova Scotia was to collect live squid, usually *I. illecebrosus*, for use in the laboratory, and therefore *L. pealei* was only recorded when sufficient numbers of healthy individuals were captured.

Ryan thermographs, moored at a depth of 11 m, were used to obtain daily bottom temperatures at Holyrood. Bottom water temperatures were not taken at the actual Nova Scotian collection sites, but could be approximated by temperatures taken at the 12 m deep Aquatron Laboratory seawater intakes (Fig. 1) in an adjacent inlet (B. Ruddick, Dalhousie University, Department of Oceanography, Halifax, N.S., pers. comm. 1987).

To determine whether the observed *L. pealei* were from a successfully spawning population, egg strings (Arnold 1962) were collected from the netting of the Nova Scotian box traps in 1986 as well as from the Aquatron Laboratory Pool Tank in which captive *L. pealei* were maintained in both 1979 and 1986. These egg strings were incubated in flowing seawater at ambient temperature to determine viability and the effect of temperature on development.

Measurements were taken of dorsal mantle lengths (ML) and nidamental gland lengths. Sex and stages of maturity were also noted. Different observers collected the data in Newfoundland and Nova Scotia, and because of the subjectivity inherent in assessing maturity indices, animals were recorded only as mature or immature. Whole animal weights were recorded in 1986.

Results

L. pealei was captured at Holyrood for the first time in 1986 (Table 1), although traps had been set there each year from 1983. In contrast, since observations commenced in Nova Sco-

TABLE 1. Years in which *Loligo pealei* were captured at Nova Scotia and Newfoundland, and, where the catch was sampled (see text), the sex composition, mean length, and length range (sex only was determined in 1979).

Year	Location	Dates	Sample size	Percent male	Mantle length (cm) Mean		Mantle length (cm) Range	
					Male	Female	Male	Female
1974	Herring Cove, Nova Scotia	Aug. 12–Sept. 17	87	98	24.2	16.0	14–34	16
1975	St. Margaret's Bay, Nova Scotia	June 17–27	110	71	34.4	25.4	19–41	23–31
1976	Herring Cove, Nova Scotia	June 24	5	40	29.5	24.3	27–32	24–26
1979	Herring Cove, Nova Scotia	June 2	30	54				
1981	Herring Cove, Nova Scotia	Aug. 27	1					
1985	St. Margaret's Bay, Nova Scotia	Oct. 25	1					
1986	St. Margaret's Bay, Nova Scotia	Sept. 25–Oct. 15	160	84	22.8	16.2	14–37	12–20
1986	Holyrood, Newfoundland	Sept. 2–Oct. 11	44	95	22.6	15.6	13–28	12–20
1986	South Dildo, Newfoundland	Sept. 10	1	100	24.0	—	24	—

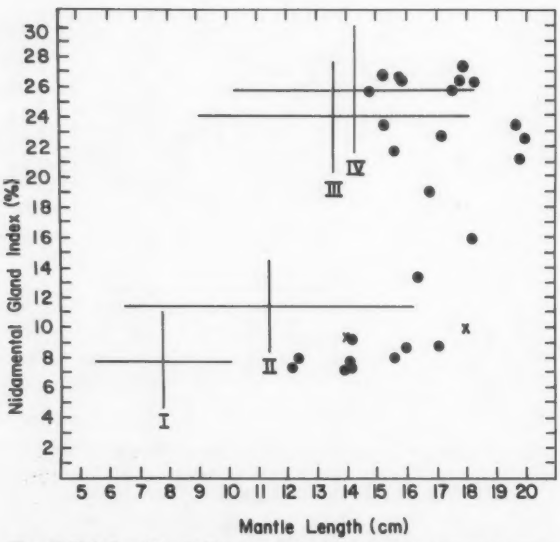

FIG. 2. Relationship of nidamental gland index (NGI) to mantle length for female *Loligo pealei* collected during the fall of 1986. The mean NGI +/− one SD for maturity stages as defined by Macy (1982) are shown. (x) Holyrood samples. (●) Nova Scotia Samples.

tia in 1974, *L. pealei* was captured there in several years between 1974 and 1986 (Table 1). That *L. pealei* was observed on the eastern coast of Nova Scotia in seven of 13 yr indicates that its presence there is not uncommon.

Males represented 71–98% of the catch in samples examined (Table 1). Observations of sexual maturity were made only in 1974 and 1986. All males collected from Newfoundland in 1986 were sexually immature, while those collected in Nova Scotia in 1974 and 1986 were a mixture of immature and mature animals. In 1986, 16 of the largest females and 114 of the males from Nova Scotia were determined from macroscopic inspection to be sexually mature upon capture. The nidamental gland index (ratio of nidamental gland length to mantle length) was plotted against each female's corresponding mantle length and compared with Macy's (1982) objective maturity stages for squid from Naragansett Bay (Fig. 2). Fourteen of the 16 Nova Scotian females which were classified as sexually mature fell in the range that Macy (1982) classified as stage 4 (sexually mature). Females in the size range 12–14.5 cm ML, including the two from Holyrood, fell within Macy's stages 1 or 2 (sexually immature).

As is commonly observed with *L. pealei*, mean lengths for males in each sample from Nova Scotia and Newfoundland were consistently greater than for females (Table 1). The 1986 males from Nova Scotia ranged from 14 to 37 cm ML, whereas females ranged from 12 to 31 cm ML (Table 1). Holyrood males ranged from 13 to 28 cm ML.

Daily bottom temperatures at the Holyrood trap when *L. pealei* were caught in 1986 were in the range of 8.5–12.6°C. At the time of the captures in Nova Scotia, temperatures were in the range of 6.4–9.5°C in the spring, and 9.5–16.9°C in the fall.

No egg strings were found in Newfoundland. In Nova Scotia, 16 egg strings were collected on October 6, 1986, spawned by *L. pealei* in the box traps in St. Margaret's Bay. Maintained in the Aquatron Laboratory Pool Tank, *L. pealei* spawned approximately 1 000 egg strings in June 1979, while 45 were collected in October 1986. In addition, *L. pealei* egg strings were photographed by a SCUBA diver in June, 1983 in Terrence Bay (Fig. 1), although these were not collected. The eggs we collected were viable as reflected in a hatching rate of about 70% for the 1979 egg strings and greater than 95% for the eggs collected in 1986. Relatively low percent hatching for spring 1979 eggs was probably related to lower incubation temperature (7.0–13.5°C) and longer incubation period (82–91 d) than for

both 1986 experiments. Eggs collected from the wild and the laboratory in 1986 were incubated at 14.5–10°C and 14.0–9.0°C for 35 and 32 d respectively.

Discussion

This report of *L. pealei* from inshore Nova Scotia extends the geographic distribution of the species northward along the east coast of Nova Scotia. Specimens collected from Holyrood and South Dildo, Newfoundland establish a new northern and eastern range extension. Since the Holyrood trap was fished consistently from 1983 to 1988, the occurrence of *L. pealei* only in 1986 suggested that its presence in Newfoundland waters was unusual. In contrast, the Nova Scotian observations between 1974 and 1986 indicated that *L. pealei* was more common there. Indeed, *L. pealei* was usually observed in the late spring and early summer. It is referred to by local Nova Scotian fishermen as the "bone squid" to distinguish it from *I. illecebrosus*.

Although sex ratios observed by us contrast with Macy's (1980) observations that sexes are approximately equal in trawl-caught samples from Narragansett Bay, our data are consistent with those of Summers (1983) who observed that sex ratios in the inshore waters of New England vary due to differences in the migrations of the two sexes. Our observations also agree with those of Mesnil (1977) that squid greater than 18–20 cm ML from Georges Bank were predominantly male.

Consistent with data from the more southern areas of the species' range, (Summers 1971, 1983; Mesnil 1977; Hixon et al. 1981; Lange and Sissenwine 1980; Macy 1980), males attained larger sizes than females. However, animals collected from Nova Scotia were generally larger than those reported from more southern waters. Indeed, a 31 cm ML female collected in 1975 was the largest reported female of this species (Summers 1969; Macy 1980; Hixon et al. 1981). This was consistent with a previously described trend for increasing mean size at maturity from south to north (Summers 1983). Water temperatures observed, especially at Holyrood, when *L. pealei* was present, were consistent with observations that the greatest catches of the species between Florida and Georges Bank were related to bottom temperatures above 8°C (Summers 1969, 1983; Serchuk and Rathjen 1974; Tibbets 1977; Whitaker 1978; Lange 1980; Macy 1980).

Reports of *L. pealei* spawning, or the presence of their paralarvae (see Young and Harman 1988 for a description of the term "paralarva") in northern waters have been limited. The most northern reported spawning has been in the Bay of Fundy in August and September (Bigelow 1924; Stevenson 1934). Paralarvae (Young and Harman 1988) have been found in Minas Basin (Cohen 1976) and Cobequid Bay (Bigelow 1924), the latter being 2–4 mm ML. *Loligo pealei* hatches at 2mm ML (Summers 1983), indicating that the paralarvae reported from Cobequid Bay were spawned there. Our observations of viable eggs spawned in St. Margarets Bay indicate that spawning also occurs as far north on the east coast of Nova Scotia. In contrast there was no evidence of spawning or of sexual maturity in either sex at Newfoundland.

McMahon and Summers (1971) showed that embryonic development for *L. pealei* is directly related to temperature; at temperatures of at least 12°C. We have shown here that survivorship to hatching approaches 100% for fall-spawned eggs exposed to temperatures as low as 9°C and 10°C. However, spring-spawned eggs from Nova Scotia, exposed to temperatures as low as 7°C, did not approach complete hatching even though they were incubated for two to three times as long as fall-spawned eggs. These observations are consistent with the suggestion of McMahon and Summers (1971) that eggs are probably deposited in nature at temperatures of at least 8°C. They noted that *L. paelei* eggs are usually found near Woods Hole from May to October when temperatures range between 0–23°C. The season for successful embryonic development must become more restricted from southwest to northeast.

Our observations of increased numbers of *L. pealei* in 1986 correspond with the fact that a catch of nearly 67 t was reported for 1986 in NAFO Subarea 4 (Fig. 1) around New Brunswick and Nova Scotia (NAFO Secretariat 1987), where traditionally there has not been a fishery dominated by *L. pealei*. Its unusual occurrence in an area with an historical fishery reportedly returning only *I. illecebrosus* suggests the possibility of unique events which may have resulted in this extension of the species' range. At least three types of changes seem plausible: (1) increased seawater temperatures in Nova Scotian and Newfoundland waters; (2) an increase in the overall population of *L. pealei* itself; and (3) changes in the biology or distribution of interacting species.

Bottom water temperature data for both the Newfoundland and Nova Scotia collection sites were not unusually warm. In fact, 1986 was the fifth consecutive year of anomalously low temperatures along the Continental Shelf of Atlantic Canada (Drinkwater and Trites 1987; Petrie et al. 1987). In addition, the frontal area of the core of the Labrador Current flowing across the Grand Bank, along 47°N latitude, was at its largest in 1986 (Petrie et al. 1987). The unusual presence of *L. pealei* cannot therefore be related to a warming trend in water temperature in these inshore areas or in waters which migrating *L. pealei* would have to penetrate to reach the collection sites in Newfoundland.

To address the question of whether the extension of *L. pealei* may have resulted from an increase in population size, resulting in its expansion into new areas, the only data available are fishery catch statistics for the entire *L. pealei* fishery (Fig. 3). These data do not indicate that the abundance of this species was greater in 1986 than in any other year (NAFO Secretariat 1986, 1987, 1988a, 1988b).

In considering species which may interact with *L. pealei* and so affect its distribution, the short-finned squid (*I. illecebrosus*) would be the most likely. It is usually the dominant squid species in Newfoundland and Nova Scotian waters and is sympatric with *L. pealei* south of Nova Scotia. The pronounced northern range extension of *L. pealei* in 1986 occurred during a year when the *I. illecebrosus* population was very low. The 1986 *I. illecebrosus* catch for Atlantic Canada (NAFO Subareas 2–4) was at its lowest since 1968, while the catch for the entire fishery, which extended from Labrador (NAFO Subarea 2) to Cape Hatteras (NAFO Subarea 6) was at its lowest since 1970 (Fig. 3; NAFO Secretariat 1986, 1988a, 1988b). Furthermore, in 1986, when *L. pealei*'s occurrence at Newfoundland was first recorded, the total inshore reported catch of *I. illecebrosus* at Newfoundland was only 1 t.

It appears that northward expansion of the *L. pealei* population may be related to low abundance of *I. illecebrosus*, and we speculate that the former species may usually be competitively excluded from such northern waters by the latter. In Nova Scotian waters, *L. pealei* has been collected within the usual season of occurrence of *I. illecebrosus* (July–November) only during years of relatively low abundance of the latter species

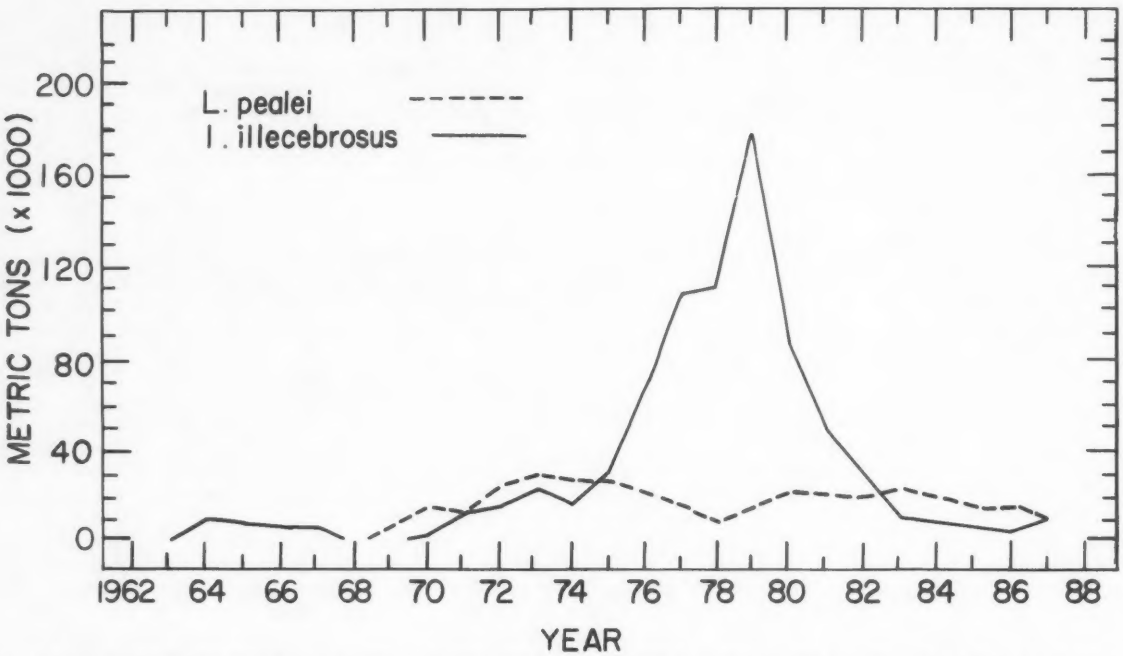

FIG. 3. Total annual catches of *Illex illecebrosus and Loligo pealei* in the Northwest Atlantic Fisheries Organization (NAFO) Subareas 2–6 for the period 1962–87 (from NAFO Secretariat 1986, 1987, 1988a, 1988b).

(1974, 1981, 1985, and 1986). In contrast, *L. pealei* collections during years of high *I. illecebrosus* abundance (1975, 1976, and 1979) have only occurred during June, earlier than *I. illecebrosus* is usually found in inshore waters. Local fishermen also observe *L. pealei* usually in late spring and early summer, which are times when *I. illecebrosus* has not yet migrated into inshore waters.

Some other observations are consistent with the theory of the northern and eastern range of *L. pealei* being limited by the abundance of *I. illecebrosus*. Neither species, as an adult, is a specialized predator, and feeding studies indicate that they may compete for the same prey (O'Dor 1983; Vinogradov and Noskov 1979, Vovk 1972; Stunkard 1977; Gaevskaya and Nigmatullin 1978; Brown and Threlfall 1968a, 1968b). Our observations of both species held simultaneously in the Aquatron Laboratory Pool Tank (unpubl. data) indicate that *I. illecebrosus* is a more aggressive predator than *L. pealei*.

Whether or not abundance of *L. pealei* is related to that of *I. illecebrosus*, it is clear that the former species may occur in large numbers in Canadian Atlantic waters, rather than merely as occasional specimens. The 1986 reported catch of *L. pealei* around Nova Scotia and New Brunswick (NAFO Subarea 4) of 67 t suggests that this species could occur in such abundance in some years as to support a small commercial fishery in Canadian waters.

Acknowledgments

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Micrograzer Impact and Substrate Limitation of Bacterioplankton in Lake Michigan

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We estimated Lake Michigan epilimnetic heterotrophic bacterial loss rates, predator size, and substrate limitation in 1986 and 1987. The bacterial growth rates were always enhanced by organic substrate additions indicating that bacterial growth is limited, to some degree, by substrate availablility. In this study we obtained loss rates and intrinsic growth rates each between 0.32 and 1.45 d^{-1}. The grazers were predominantly picoplankton-size organisms, presumably heterotrophic flagellates. Using radiolabeled bacteria, only a small percentage (2–3%) of bacterial cells were incorporated into larger size fractions after 24 h. These results indicate that during our experiments heterotrophic bacteria were not a direct, significant, carbon source for the upper trophic levels.

Nous avons évalué le taux de déperdition des bactéries épilimnétiques hétérotrophes, la taille de leurs prédateurs et les contraintes imposées à leur croissance par les ressources nutritives auxquelles elles ont accès dans le lac Michigan en 1986 et 1987. L'addition de matière organique avait toujours pour effet d'accroître les taux de croissance des bactéries, ce qui laisse entendre que leur croissance dépend, dans une certaine mesure, de la quantité de substrat à laquelle elles ont accès. Les taux de déperdition et de croissance intrinsèque que nous avons obtenus se situaient chacun entre 0,32 et 1,43 $jour^{-1}$. Les organismes de taille picoplanctonique, probablement des flagellés hétérotrophes, étaient les principaux brouteurs. Au moyen de bactéries radiomarquées, nous avons observé que seulement un faible pourcentage de cellules bactériennes (2–3%) était incorporé dans des organismes de plus grande taille 24 heures après le début de l'expérience. Ces résultats montrent que, durant nos expériences, les bactéries hétérotrophes ne constituaient pas une source directe importante de carbone pour les organismes des niveaux trophiques supérieurs.

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The roles of both heterotrophic and autotrophic picoplankton in aquatic food webs are increasingly recognized as ecologically significant. For example, several studies have found that much of the carbon assimilated by heterotrophic bacteria and autotrophic picoplankton is grazed by nano- and microplankton populations (e.g. >3μm protozoans) (Wright and Coffin 1984; Fahnenstiel et al. 1986; Pace 1988; Gude 1988). In the Upper Great Lakes the importance of picoplankton may be especially signficiant because at times heterotrophic bacterial production rates rival autotrophic production in Lake Michigan (Scavia et al. 1986; Scavia and Laird 1987) and nearly half of autotrophic primary production passes a 3.0 μm screen in Lake Superior (Fahnenstiel et al. 1986). Marine studies have also found that a substantial proportion of the autotrophic production is associated with particles passing a 1.0 μm screen (Li et al. 1983). While there is significant activity in the microbial food web, it is still unclear if significant carbon is passing from this loop to the traditional food web (i.e. crustacean zooplankton, nano- and net phytoplankton). This question will have to be addressed to further understand the role of picoplankton in the ecosystem.

We suggested in earlier work (Scavia and Laird 1987) that grazing is the dominant process in controlling the size of the rather stable Lake Michigan heterotrophic bacteria population. Recently it was found that surface abundances of nanoflagellates peaked during mid-stratification (Carrick and Fahnenstiel 1989), a period when bacterial abundances decline (Scavia and Laird 1987). This further indicates a tight coupling between the nanoplankton and picoplankton populations.

Substrate availability appears to be an important factor controlling epilimnetic bacterial growth in Lake Michigan (Scavia and Laird 1987; Gardner et al. 1986, 1989). Because bacteria

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are considered to be the link between the dissolved organic pools and the traditional food web, the quantitative importance of bacterial substrate limitation would improve the overall understanding of the microbial food web.

In this study we made seasonal estimates of bacterial grazing rates. In 1987, fractionation experiments were also conducted to estimate the percentage of bacteria transferred to the mesoplankton via the microbial food web and also determine predator size. Finally, we used substrate addition experiments to determine if and when bacterial growth could be stimulated by increasing available organic carbon.

Methods

Sample location was at the 100-m depth contour, 26 km west of Grand Haven, Michigan (43°1′11″N, 86°36′48″W). Surface (5 m) water samples, taken aboard the R/V *Shenehon*, were transferred to a 4-L or 20-L carboys and processed either on board or stored in coolers in the dark for no more than 3 h before processing at shore.

All experimental treatments were incubated 8–10 h in the dark at ambient temperature and subsampled for bacterial abundance over time. Subsamples ($n = 3$–10) were preserved (2% formaldehyde final concentration), and bacteria were counted by acridine orange direct count (AODC) method (Hobbie et al. 1977).

In 1986 experiments were done eight times in 1-L and 2-L precombusted BOD bottles on raw lakewater. In June and August of 1987 they were done in duplicate 2-L sterile tissue culture flasks (Corning tissue culture bottles, 850 cm^2) and sample water was prefiltered through a 35 μm Nitex screen. Rates of change in bacterial cell abundance were determined from linear regression of ln (abundance) vs. time.

To estimate grazing loss rates, one treatment in each experiment received the antibiotic gentamicin (Sigma, cat. no. AA-5-18, 20 μm mL^{-1} final concentration) at the beginning of the incubation. The antibiotic stops bacterial growth; thus, rate of decline in cell abundance (r_A), which represents total bacterial mortality, is assumed to be due to grazing. For comparison, two separate treatments received 0.61 μm non-carboxylated fluorescence beads (mean volume = 0.12 μm^3, SD = 4×10^{-5} μm^3, final concentration 10^5 beads mL^{-1}, Polysscience). Bacterial cells in Lake Michigan summer epilimnetic regions are approximately 0.072 μm^3 in size (Scavia and Laird 1987). One of these two samples received the antibiotic gentamicin as well as beads. We compared the rate of disappearance of beads in these two samples to each other and to the independent estimate r_A. In 1987 we included a second control in which beads were added to 0.2 μm filtered (Nuclepore) water. The disappearance of beads in this treatment was attributed to abiotic factors such as sorption to the walls of the container.

Intrinsic growth rates (μ) can be calculated from the slope of ln(bacteria abundances) vs. time in the untreated sample, r_R, and the slope of ln(bacterial abundances) vs. time in the antibiotic treated sample, r_A. The realized population growth rate, r_R, is equal to the difference between intrinsic growth rate, μ, and loss (m) rate:

$$(1) \quad r_R = \mu - m.$$

Because growth is inhibited ($\mu = 0$), r_A is equal to $-m$; this loss rate has been attributed to grazing (Fuhrman and McManus 1984; Scavia et al. 1986). By determining r_R and r_A, we can calculate an intrinsic growth rate from

$$(2) \quad \mu = (r_R + m) = (r_R - r_A).$$

To explore the size range of potential predators, lake water was also gently filtered through 0.8, 1.2, 2.0–5.0, or 10.0 μm 47 mm-diameter Nuclepore filters prior to incubation.

In the substrate addition experiments, both glucose (final concn. 0.522 μM) and a mixture of 17 amino acids (Sigma, cat. no. AA-S-18, final concn., 0.522 μM) were added to raw lake water. Change in bacterial abundance was followed over time as above.

In 1987 experiments, the flux of bacterial cells into larger size fractions was determined using both radiolabeled planktonic bacteria derived from Lake Michigan and radiolabeled "minicells" derived from a mutant strain of *Escherichia coli*. During cell division of specific *E. coli*, a small spherical "minicell" is produced containing no DNA, as well as a normal cell with a full complement of DNA (Wikner et al. 1986). We used these two types of tracer bacteria to overcome some of the limitations of each. Radiolabeled planktonic bacteria, while accurately representing diversity of sizes and shapes of natural bacteria, would probably not become uniformly labeled in the short incubations we used (see below). Minicells, on the other hand, represent only a single size and shape, but offer the advantage of being uniformly labeled.

Planktonic bacteria for radiolabeling were concentrated from 6 L of lake water by first gently filtering through a 1.0 μm Nuclepore filter. Amino acids were added (Sigma, cat. no AA-S-18, 20 μg·mL^{-1}final concn.) to the 1.0 μm filtrate to ensure that ample substrate was available for bacterial growth. The filtrate was concentrated through reverse filtration using a 4-L pressure tank and a stirring cell filled with a 0.2 μm 76 mm Nuclepore filter resulting in a 6-fold concentration. The concentrate was incubated for 1 h at epilimnetic temperature before 1 mCi of [^{3}H-methyl]thymidine (70–80 Ci·$mmol^{-1}$, New England Nuclear) was added and incubated for one additional hour. Two 20-L polycarbonate carboys were filled with unaltered lake water and unlabeled thymidine (final concentration 3.0 nM). The radiolabeled concentrate was split and added to both 20-L carboys (4% of ambient concentration).

We used a modification of the method of Wikner et al. (1986) to radiolabel minicells. Minicells were isolated from larger cells in overnight cultures using sucrose gradient centrifugation (Wikner et al. 1986). Minicell suspensions concentrated in a buffered saline solution (BSG — 0.85% NaCl, 0.03% KH_2PO_4, 0.06% Na_2HPO_4 100 μg gelatin·mL^{-1}) were incubated with 250 μCi [^{3}H]methionine (80 Ci $mmol^{-1}$) in a shaking water bath at 37°C overnight. To remove unincorporated radioactivity, cells were sedimented by centrifugation and resuspended in BSG. Radioactivity per cell was determined by filtering 0.1 mL of the final minicell suspension on a 0.2 μm Nucleopore filter. Filters were washed twice with BSG, added to a scintillation vial, boiled for 1 h in 5% trichloracetic acid, and radioassayed. Minicell concentrations were determined by enumeration using the acridine orange direct count method (Hobbie et al. 1977). Minicells were added to single 20 L carboys at 7–8 × 10^5 minicells·mL^{-1} (= 2–4 × 10^3 DPM·mL^{-1}).

The 20-L carboys containing either radiolabeled minicells or concentrated radiolabeled planktonic bacteria were incubated at shore under screened natural light and epilimnetic temperatures. After 24 h, the contents of the 20-L carboys were filtered sequentially through 100 μm and 35 μm Nitex screens and

TABLE 1. Ingestion rate of florescent beads, d^{-1}. NS — Non-significant regression.

Date	Lakewater Rate	SE	Antibiotic treated Rate	SE	Average[a]
4/30/86	0.42	0.17	0.54	0.19	0.48
5/27/86	1.20	0.43	1.50	0.38	1.35
6/12/86	0.34	0.15	0.63	0.04	0.49
7/2/86	0.65	0.20	NS		0.65
7/28/86	NS		0.32	0.16	0.32
8/21/86	1.45	0.60	1.12	0.26	1.29
10/3/86	0.67	0.21	0.33	0.21	0.50
10/23/86	1.70	0.84	1.64	0.93	1.67

[a]Slopes with and without antibiotic treatments were not significantly different ($\alpha = 0.10$).

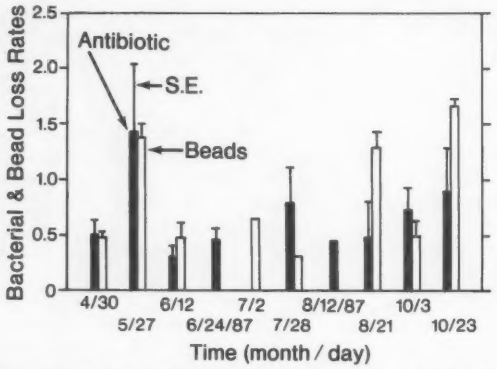

FIG. 1. Bacterial and bead loss rates (d^{-1}) in 1986 and 1987. Bead rates represent the means of treatments with and without antibiotic. Error bars represent standard error of regression.

through 10.0, 2.0, and 0.2 μm Nuclepore filters. An additional filter (0.8 μm) was used in the August 1987 experiment. The Nuclepore filters and subsamples of the 35 μm filtrate were placed in liquid scintillation vials. Material caught on the Nitex screens was washed onto 10 μm Nuclepore filters and placed in vials.

Twelve mL's of Filter Count (Packard) scintillation cocktail were added to each scintillation vial and radioactivity was assayed with a Packard Tri-Carb scintillation spectrometer. Counting efficiency was determined with external standards.

Results

Our method of estimating grazing rates assumes that the antibiotic, gentamicin, does not effect the eucaryotic grazers. To evaluate this, we measured the disappearance rates of bacteria-sized fluorescence beads in lake water with and without gentamicin. These measurements may underestimate actual rates because our incubation times (8–10 h) were significantly greater than gut retention times (20–60 min) of protozoa (Sherr et al. 1988). However, our estimates are based on regressions of time-course measurements and we observed no systematic decrease in rate estimates over time. In general, the disappearance rates with and without gentamicin were not significantly different (Table 1). Therefore, for further comparisons (see below) we averaged the two rates. In 1986 disappearance rates ranged from 0.32 to 1.67 d^{-1} (Table 1, Fig. 1). As a control, beads were also added to 0.2 μm filtrate during the 1987 experiments. The rate of bead disappearance in these filtrates was 0.70 d^{-1} on June 24 and 0.37 d^{-1} on August 12. These rates were subtracted from the disappearance rates of beads in untreated lake water (0.96 d^{-1} and 0.77 d^{-1}, respectively). Because the filtrate loss rates in these experiments were high, we repeated these filtrate-control experiments both in the combusted glass BOD bottles, used in 1986, and in the tissue culture flasks, used in 1987. In both cases there was no significant rate of change in bead abundances ($\alpha > 0.40$); therefore, we assume that the 1987 results were specific to that experiment. Bacterial loss rates, based on the antibiotic treatment, ranged from 0.32 to 1.43 d^{-1} in 1986 and were 0.48 d^{-1} on both June 24 and August 12, 1987 (Table 2, Fig. 1).

To determine the size of potential predators, lake water was prefiltered through several different filter pore sizes prior to incubation. The increase in bacterial abundance, above that found in the unaltered treatments, was attributed to predator elimination. In 1986, when filtrate sizes ranged from 2–5 μm, a significant increase in bacterial population occurred only in October. On June 24, 1987 several filter sizes were used. In the 2.0 μm-filter, 10.0 μm-filter, and untreated samples, the rate of change in abundances was not significantly different from zero. In the 0.8 μm-filter and 1.2 μm-filter treatments, growth rates of 0.48 ± 0.07 d^{-1} and 0.66 ± 0.18 d^{-1} (rate ± SE) were found, respectively, On August 12, 1987 growth rates of 0.35 ± 0.10 d^{-1} and 0.14 ± 0.10 d^{-1} (rates ± SE) were obtained in replicate 0.8 μm filtrates. Generally, we found that only in the less than 2.0 μm-filtrates was there a significant positive increase in bacterial abundances above those of the unaltered samples. This suggested that the predators are in the less than 2.0 μm size category.

These results were confirmed with the tracer experiments in which radiolabeled bacteria traced consumption into various size fractions of the food web. After 24 h, very little isotope was found in size fractions greater than 2.0 μm either in the case of treatments using concentrated lake bacteria or minicells. On June 24, 97% (concentrated bacteria) and 85% (minicells) of the label remained in the 0.2–2μm fraction (Fig. 2a). On August 12, for the concentrated bacteria treatment, 80% remained in the 0.8 μm fraction (Fig. 2b). Similarly, for the minicell treatment in August, 95% of the label remained in the smallest two size fractions (Fig. 2b).

We inferred substrate limitation if added substrate stimulated bacterial growth rates above the unaltered controls. In 1986 growth rates ranged between 0.29 and 1.11 d^{-1} in the lake water samples receiving substrate (Table 2). In 1987 growth rates in two separate experiments were 0.48 and 1.20 d^{-1} on June 24, and 0.33 d^{-1} on August 12. These rates are all greater than those in the respective controls.

Discussion

Substrate Limited Growth

We have shown previously for Lake Michigan that below 10°C bacterial growth rate increases logarithmically with increasing temperature (Scavia and Laird 1987). These conditions exist for subthermocline regions all year and for the entire water column between early fall and spring. When temperatures are warmer, growth appears to be limited more by substrate availability. Gardner et al. (1987) evaluated this for Lake Michigan bacteria by comparing seasonal

TABLE 2. Grazing and growth rates (d^{-1}). r_R = Control, bacterial growth rates; r_A = antibiotic treatment, bacterial mortality rates; r_S = substrate addition, bacterial growth rates; SE = standard error of regression slope; P = attained level of significance of regression; NS = non-significant regression.

	Untreated			Antibiotic			Substrate addition		
Date	r_R	SE	p	r_A	SE	p	r_S	SE	p
4/30/86		NS		0.51	0.09	0.03	1.11	0.39	0.10
5/27/86		NS		1.43	0.59	0.14	0.52	0.35	0.28
6/12/86		NS		0.32	0.10	0.05	0.49	0.29	0.19
7/2/86		NS			NS		0.29	0.15	0.15
7/28/86		NS		0.79	0.31	0.09	0.48	0.03	0.005
8/21/86		NS		0.49	0.30	0.24	1.10	0.11	0.06
10/3/86	−0.28	0.02	0.05	0.74	0.19	0.06	0.55	0.37	0.28
10/23/86				0.90	0.38	0.14			
6/24/87		NS		0.48	0.07	0.001	0.48	0.24	0.08
							1.20	0.14	0.0003
8/12/87	0.17	0.10	0.14	0.48	0.07	0.001	0.50	0.24	0.11
		NS		0.48	0.19	0.06			

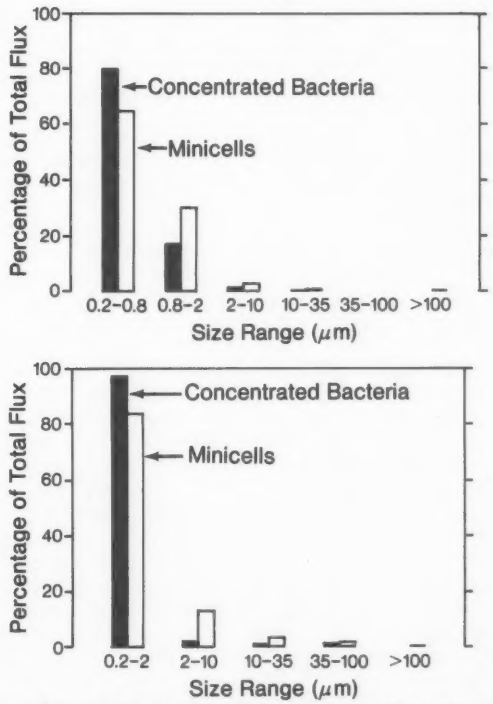

FIG. 2. Percent of total radiolabeled bacteria found in various size fractions after 24 h incubation. (a) June 24, 1987 and (b) August 12, 1987.

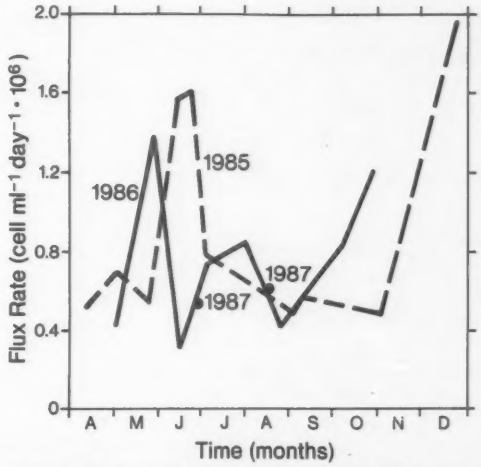

FIG. 3. Bacterial flux rates (cell·mL^{-1}·day^{-1}) calculated from specific loss rates and ambient cell concentrations in 1985, 1986, and 1987.

"maximum" and "actual" dissolved free amino acids (DFAA) turnover rates. In their analysis, the greater the difference between the two rates the greater the substrate limitation. They found the greatest differences in summer and early fall, suggesting that bacteria are more limited by substrate in the summer epilimnion than during spring and fall. In contrast, we have shown lowest response of bacteria to added organic substrates (glucose plus DFAA) to occur in midsummer (Table 2). Both of these methods rely on following a response to presumably important substrates. More recently, Laird and Scavia (1990) have followed the seasonal development of bacterial growth potential on natural organic supplies and found, similar to Gardner et al. (1989), that the substrate supply appears to dwindle over summer.

Grazing Losses

Use of antibiotics to inhibit bacterial growth and estimate grazing loss presumes that the decreases in population size, which represents total bacterial mortality, are mostly due to grazing and that the antibiotic is specific to prokaryotes. Previously, we showed that gentamicin alone does not cause a decline in bacterial cell abundance (Scavia et al. 1986). In this study, we demonstrated that the ingestion of bacterial-size fluorescence beads was not influenced by the addition of gentamicin. Therefore, we conclude that the predators in the presence of gentamicin continued to ingest bacteria normally.

In this study, we also used selective filtration to estimate predator size. Problems with this technique potentially include the introduction of dissolved organic compounds in the filtrate, presumably as a result of cell breakage (Goldman and Dennett 1985), removal of phytoplankton that supply organic carbon to the bacteria, and removal of some of the bacterial population.

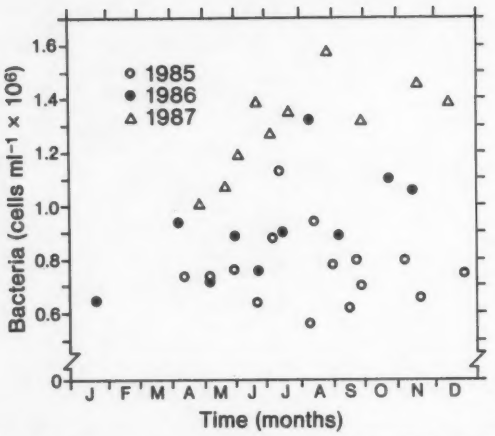

FIG. 4. Surface water bacteria abundances in 1985, 1986, and 1987.

TABLE 3. Flux and clearance rates for 1986 and 1987

	Clearance rates $nL \cdot cell^{-1} \cdot h^{-1}$	Flux rates 10^5 cell·mL^{-1}·d^{-1}
4/30/86	9.4	4.40
5/27/86	15.9	13.91
6/1/86	2.4	3.13
7/28/86	3.8	8.61
8/21/86	2.9	4.55
10/3/86	8.2	8.42
10/23/86	10.0	11.97
6/24/87	3.6	5.42
8/12/87	2.8	6.19

Initial bacterial abundances in the filtrate experiments were similar to those in lake water; therefore, the latter problem did not seem major. Further, it has been demonstrated that there is no increase in measurable primary amine or ammonium concentration in Nuclepore-filtered Lake Michigan water (Gardner et al. 1987). Removing algae could potentially reduce bacterial production; however, we could not assess that effect with the methods used in this study.

Grazing loss rates ranged between 0.32 d^{-1} and 1.43 d^{-1} between April and October, 1986, and were 0.48 d^{-1} on both June 24, and August 12, 1987. While these rates ranged slightly lower than those previously reported for Lake Michigan (0.62 d^{-1} – 2.8 d^{-1}; Scavia and Laird 1987) they were generally consistent with rates of loss of fluorescent beads (Fig. 1) measured concurrently. It is curious to note that while the specific loss rates in 1986 and 1987 were lower than those in 1985, higher bacterial abundances in 1986 and 1987 (Fig. 4) compensated and resulted in consistent calculated flux rates. These calculated flux rates, determined from epilimnetic bacterial abundances and experimental loss rates (r_A) (Fig. 3), ranged between 3.13 and 13.90 × 10^5 cells ingested·mL^{-1}·day^{-1} in 1986 and 1987. Flux rates in 1985 were 4.95 – 21.2 × 10^5 cells ingested·mL^{-1}·day^{-1} (Scavia and Laird 1987). Flux rates peaked during late spring when bacterial production is also highest (Scavia and Laird 1987), declined during summer, and increased again in the fall.

Predators appeared to pass through the 2–5μm filter used in 1986. This is consistent with filtrate experiments in 1987 when significant increases in cell abundances occurred only in the less than 2.0 μm size filtrate. Marine studies have also suggested that the major consumers of bacteria are small heterotrophic flagellates (Fenchel 1982a; Fenchel 1986). A recent experimental study by Wikner and Hagstrom (1988) found results similar to ours for coastal marine environments. In their study, predation on bacteria was measured in a series of size fractionated water samples. Predation was generally reduced only by filtration though 1.0 and 0.6 μm filters, implying that the primary predators were flagellates in the size range of 1–3 μm.

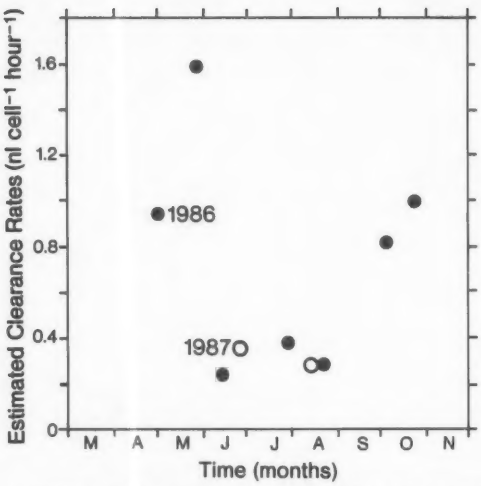

FIG. 5. Estimated clearance rates (nL·flagellate^{-1}·day^{-1}) calculated from specific loss rates and heterotrophic flagellate abundance estimates from Carrick and Fahnenstiel (1989).

In our tracer, bacteria experiments we found <5% of the label in size classes greater than 2.0 μm after 24 h (Fig. 2a, 2b). Both types of tracers, concentrated lake bacteria and minicells, showed the same pattern, suggesting our conclusion is not limited by methodological concerns over labeling natural communites or using a single type of tracer cell. A similar study followed the fate of ^{14}C-labeled bacterioplankton and found that only 2% of the labeled bacterial cells were present in the larger organisms (Ducklow et al. 1986) after 13 d. Both studies indicate that heterotrophic bacterial carbon may not be passed significantly up the food chain, and that the primary bacteria consumers, the nannoflagellates, provide a formidable block in the carbon flow. Further investigations are needed to substantiate this conclusion.

To explore the notion that the heterotrophic flagellates are responsible for the bactivory in Lake Michigan, we calculated clearance rates from our estimated specific grazing rates and flagellate abundances determined in Lake Michigan surface waters in 1987 (Carrick and Fahnenstiel 1989). These estimates for summer ranged between 2.4 and 3.8 nL·flagellate^{-1}·hr^{-1} and are similar to those reported elsewhere (0.3-1.0 nL·flagellate^{-1}·h^{-1}, Sherr et al. 1983; 2.3–4.4 nL·flagellate^{-1}·h^{-1}, Caron et al. 1985; 4.2–12.9 nL·flagellate^{-1}·h^{-1}, Goldman and Caron 1985). Clearance rates in spring and fall 1986 were higher (8.2–15.9 nL·flagellate^{-1}·hr^{-1}) and similar to those of larger marine species (2–40nL·flagellate^{-1}·h^{-1}, Fenchel 1982b; 15–20nL·flagellate^{-1}·h^{-1}, Anderson and Fenchel 1985) (Table 3; Fig. 5). It thus seems reasonable to assume that the flagellates enumerated by Carrick and Fahnenstiel (1989) are

responsible for the bacterial grazing loss rates, although the possibility of consumption of bacteria by small mixotrophic algae (Sander and Porter 1988) cannot be excluded at present.

In conclusion, Lake Michigan epilimnetic bacterial growth rates can be stimulated by organic substrate between April and October. Bacterial growth is often in balance with bacterial loss and the immediate bacterial grazers fall into the picoplankton size category (0.2 μm – 2.0 μm). We found that bacterial carbon does not pass quickly to higher trophic levels, within a 24 h period, indicating that bacterial production may be a sink rather than a significant source of carbon for the upper food web in Lake Michigan.

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ANNOUNCEMENTS/AVIS

Third International Workshop on Phosphorus in Sediments

The Third International Workshop on Phosphorus in Sediments will be held in Woudschoten, The Netherlands from September 30th to October 3rd 1991. Scientific sessions will include both oral and poster presentations and will cover all aspects of phosphorus dynamics in sediments.

Plenary keynote lectures will be presented:

- Dr. L. E. Fox, Harvard University, U.S.A.: *Chemical transformations of phosphorus in sediments particularly with respect to exchange processes and permanent fixation.*
- Dr. L. Lijklema, Agricultural University, The Netherlands: *Sediment-water dynamics with special attention for functional models describing fluxes of phosphorus over the sediment water interface.*
- Dr. R. Gächter, EAWAG, Switserland: *The role of microorganisms in sediment phosphorus dynamics in relation to mobilization and fixation of phosphorus.*
- Dr. G. D. Cooke, Kent State University, U.S.A.: *Water management measures focussed on the regulation of the phosphorus release from sediments, in relation to functioning and restoration of the whole ecosystem.*

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Troisième atelier international du phosphore dans les sédiments

Le Troisième atelier international du phosphore dans les sédiments aura lieu à Woudschoten, aux Pays-Bas, du 30 septembre au 3 octobre 1991. Le programme scientifique comprendra des présentations orales de même que des séances d'affichage et couvrira tous les aspects de la dynamique du phosphore dans les sédiments.

Les principales conférences plénières seront les suivantes :

- *Transformations chimiques du phosphore dans les sédiments, particulièrement en ce qui a trait aux processus d'échange et à la fixation permanente.* D[r] L. E. Fox, Université Harvard, U.S.A.
- *Dynamique sédiment-eau; intérêt particulier porté aux modèles fonctionnels décrivant les flux de phosphore dans l'interface sédiment-eau.* D[r] L. Lijklema, Agricultural University, Pays-Bas.
- *Le rôle des microorganismes dans la dynamique du phosphore sédimentaire par rapport à la mobilisation et à la fixation du phosphore.* D[r] R. Gächter, EAWAG, Suisse.
- *Mesures de gestion de l'eau axées sur la régulation de la libération du phosphore des sédiments, par rapport au fonctionnement et à la restauration de l'écosystème global.* D[r] G. D. Cooke, Université Kent State, U.S.A.

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"THE THREATENED WORLD OF FISH"
International Congress of Ichthyology, The Hague
The Netherlands, August 26-30, 1991

The 7th International Ichthyological Congress of the European Ichthyological Union (EIU) will be organized in the Congress Centre "Nederlands Congresgebouw" in The Hauge, The Netherlands from August 26–30, 1991. The scientific programme will comprise plenary lectures, parallel symposia, free and poster sessions. Many of these will be devoted to the theme of the congress:

"THE THREATENED WORLD OF FISH"

Symposia topics will be:

- Are the major fish faunas well known?
- Management and conservation of fish faunas.
- Taxonomy/Zoogeography/Phylogenetics.
- Functional and ecological morphology.
- Life history strategies.
- Applied fish biology.
- Diseases and parasites.
- Genetics and population ecology.
- Neuro-ethology and sensory physiology.
- Endocrinology and reproduction.
- Natural and anthropogenic perturbations of fish faunas.
- Multidisciplinary approach to cichlid fishes.
- Comparative anatomy.
- Behavioural and physiological ecology.
- Community ecology.
- Fish culture.
- Marine fishes and fish larvae.
- Evolutionary and applied cytogenetics.
- Recruitment.

The official language during the congress will be English, and proceedings will be published (possibly as an issue of the "Netherlands Journal of Zoology") containing lectures of about 35 invited speakers. Information concerning the scientific programme: *Dr. H. Nijssen, P.O. Box 4766, 1009 AT AMSTERDAM, The Netherlands*. Phone: +31-205256615; Telefax: +31-205257238.

The registration fee will be appr. Dfl 450, — (Dutch Guilders); students appr. Dfl 210, —. Preregistration is strongly encouraged and can be made at reduced fees (appr. Dfl 400, — for regulars, and appr. Dfl 160, — for students) until May 1, 1991. The final announcement – including registration form, accommodation form and abstract form - will be forwarded in November 1990.

It can be obtained from : *Congress Organization Services*
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THE THREATENED WORLD OF FISH
Congrès international d'ichtyologie
La Haye, Pays-Bas
du 26 au 30 août 1991

Le septième congrès international d'ichtyologie de l'*European Ichthyological Union* (EIU) aura lieu au centre de congrès *Nederlands Congresgebouw* à La Haye, aux Pays-Bas, du 26 au 30 août 1991. Le programme scientifique comprendra des conférences plénières, des symposiums parallèles, des séances libres et des séances d'affichage. Bon nombre des rencontres seront consacrées au thème du congrès :

THE THREATENED WORLD OF FISH

Les symposiums porteront sur les sujets suivants :

- Les principales faunes piscicoles sont-elles bien connues?
- Gestion et conservation des faunes piscicoles
- Taxinomie-Zoogéographie-Phylogénétique
- Morphologie fonctionnelle et écologique
- Stratégies relatives à l'histoire de la vie
- Ichtyobiologie appliquée
- Maladies et parasites
- Génétique et écologie des populations
- Neuro-éthologie et physiologie sensorielle
- Endocrinologie et reproduction
- Perturbations naturelles et anthropogènes des faunes piscicoles
- Approches multidisciplinaires des cichlidés
- Anatomie comparée
- Écologie comportementale et physiologique
- Écologie de la communauté
- Pisciculture
- Poissons marins et larves de poissons
- Cytogénétique évolutive et appliquée
- Recrutement

L'anglais est la langue officielle du congrès et les travaux seront publiés, probablement dans le *Netherlands Journal of Zoology*. Pour obtenir de plus amples renseignements au sujet du programme scientifique, s'adresser au *Dr H. Nijssen, P.O. Box 4766, 1009 AT AMSTERDAM, Pays-Bas*. Téléphone : +31-205256615; facsimile : +31-205257238.

Les frais d'inscription seront d'environ fl. 450,- (florins); étudiants : environ fl.210,-. La préinscription est fortement recommandée; les frais sont réduits à environ fl.400,- (fl.160,- pour les étudiants) jusqu'au 1er mai 1991. L'avis final - y compris les formulaires d'inscription, d'hébergement et de résumés - sera expédié en novembre 1990.

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